Aquatic macrophyte ecology in the upper Winnebago pool lakes, Wisconsin. No. 182 1993

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Aquatic Macrophyte Ecology in the Upper Winnebago Pool Lakes, Wisconsin

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Cover: A. Linde

ABSTRACT

Since impoundment in the 1850s, thousands of acres of aquatic and wet meadow vegetation have disappeared from the Upper Winnebago Pool Lakes (UWPL) of Poygan, Winneconne, and Butte des Morts and from adjacent areas. Several periods of rapidly declining macrophytes (the last one occurring in the 1960s) led to a large, turbid, open-water system by the 1970s. In response to this severe habitat degradation and uncertainty about decimating factors, a study was undertaken from 1974-82 to investigate historical changes since impoundment, and general abundance, ecology, and factors limiting macrophytes in the UWPL.

Changes in abundance of macrophytes were assessed from historical records and compared to annual and seasonal water level changes from U.S. Army Corps of Engineers' records. Aerial photography, surveys by boat, and rake sampling transects provided information on present abundance and distribution of macrophytes, growth and phenological stages, water depth tolerances, and sediment relationships. Investigation of factors that affected abundance of macrophytes included assessment of annual water level and water clarity variations, sources of turbidity, physical impact of waves and common carp, and insect infestation of bulrushes.

Long-term high water levels and extreme seasonal fluctuations (especially an amplified frequency and magnitude of flooding) after impoundment, coupled with severe wave and ice action, destroyed thousands of acres of macrophytes in the UWPL in the late 1800s and early 1900s. Additional factors, including eutrophication, sedimentation, and undesirable fish (primarily carp and freshwater drum) interacting with the initial decimating agents led to a slow decline in macrophytes during the 1930-60 period. An accelerated decline occurred during the 1960s, possibly due to extreme flooding and water turbidity in several years.

Important macrophytes in the UWPL during 1975-82 included wildrice, common reed, round-stemmed bulrushes, wildcelery, and sago pondweed. Wildrice abundance varied considerably among sites and years in 8 major stands totaling approximately 350-475 acres in 1976-78. Small, widely scattered stands of common reed and round-stemmed bulrushes were present during this study. Of these, the mid-lake stands of common reed remained quite stable. Lakes Butte des Morts and Poygan supported approximately 1,650 acres of submerged macrophytes in 8 major beds, but the abundance of these macrophytes appeared to vary inconsistently among beds and years from 1975 to 1981.

The primary factors limiting overall abundance of macrophytes during this study likely included high spring-summer water levels, abnormal timing and magnitude of water level fluctuations, and turbidity. Consistently high water levels in May and June of 1975-84 probably controlled abundance of most emergent macrophytes system-wide. Rapidly rising water levels during the floating-leaf stage throughout June and early July apparently determined system-wide abundance of wildrice. A revised water level management plan implemented in 1982 failed to reduce late spring and early summer water levels.

Low light availability (restricted by water turbidity and epiphyte communities) apparently was the ultimate limiting factor determining long-term, system-wide abundance of submerged macrophytes. Poor water clarity and high water levels in May-June limited the distribution of submerged macrophytes to maximum summer depths of 55-61 inches in Lake Poygan and 47-53 inches in Lake Butte des Morts. These maximum depth limits approximated the 5% photic zone for Lake Poygan (57-67 inches) and the 5-10% photic zone for Lake Butte des Morts (46-60 inches). However, because of consistently high turbidity throughout the study, late spring and early summer water levels determined the amount of lake bottom within the photic zone, and thus the annual abundance of submerged macrophytes. Primary sources of turbidity for Lake Butte des Morts included the Fox River, the Wolf River at Winneconne, lesser tributaries, and in-lake phytoplankton populations. For Lake Poygan, in-lake sources and lesser tributaries accounted for most turbidity.

Sediments and undesirable fish—primarily carp and freshwater drum—may be more important sources of nutrients than external sources leading to high phytoplankton and epiphyte communities. Wave action and undesirable fish probably have a greater impact on submerged macrophytes in the UWPL by contributing to turbidity than through direct physical damage to plants. Injury to new shoots and rhizomes by wave action, boats, and undesirable fish may restrict expansion of established stands or prevent re-establishment of perennial emergents in some locations. Furthermore, wave action severely erodes unprotected shorelines, adjacent marshes, and shallow littoral sediments.

Management recommendations are: (1) revise the water level management plan by establishing a new spring-summer target level under 2.5 ft at the Oshkosh gage, but allow periodic seasonal and annual fluctuations above and below this level to simulate seasonal and longer-term drought and flooding phases of a natural hydrologic cycle; also moderating winter drawdowns; (2) continue research to identify sources of turbidity and nutrients, especially from nonpoint sources including tributaries, lakeshore and side-channel developments, sediments, wave action, and undesirable fish; (3) determine factors limiting expansion of existing emergent macrophyte stands, especially long-term high water levels and extreme short-term fluctuations, wave action, boats, and undesirable fish; (4) develop and implement watershed and lake management plans, including large-scale breakwater projects to reduce water turbidity and improve water level management; (5) monitor water quality, macrophytes, and shoreline erosion to evaluate management efforts; and (6) evaluate harvest and planting techniques for propagules of macrophyte species important to these lakes.

Aquatic Macrophyte Ecology in the Upper Winnebago Pool Lakes, Wisconsin

By Rich Kahl

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CONTENTS

Large shallow littoral areas supported dense stands of emergent macrophytes in the Upper Winnebago Pool Lakes in the early 1900s which provided excellent migrational habitat for waterfowl such as this in western Lake Butte des Morts in 1912.

PHOTO: WINNECONNE HISTORICAL SOCIETY

INTRODUCTION

Management of the Upper Winnebago Pool Lakes (UWPL) of Butte des Morts, Winneconne, and Poygan for fish and wildlife is tantamount to management of macrophyte communities in this large shallow-lake ecosystem. Yet, uncertainty over causes of a major decline in macrophytes and factors preventing their recolonization of most areas hinders effective management of this unique and valuable resource.

From the late 1800s through the 1950s, the UWPL supported lush stands of emergent and submerged macrophytes and provided optimum migrational habitat for many waterfowl species, especially canvasbacks (Zimmerman 1953, Jahn and Hunt 1964, Linde 1979). In conjunction with abundant adjacent marsh habitat, these lakes also furnished prime breeding and migrational habitat for many other species of waterfowl and water birds. By the late 1960s, most of the macrophytes and adjacent marshland had disappeared. Subsequently, waterfowl migrational populations also declined precipitously (G. Jolin, Wis. Dep. Nat. Resour., unpubl. data).

Artificially high water levels and extreme seasonal and annual fluctuations were widely suggested as major decimating factors in these lakes. However, primary determinants of distribution and abundance of macrophytes elsewhere included water depth and water level fluctuations (Sculthorpe 1971), water clarity (Spence 1982, Chambers and Kalff 1985, Barko et al. 1986), epiphytic communities (Wetzel and Neckles 1986), exposure to wave action (Sculthorpe 1971, Jupp and Spence 1977), carp (Threinen and Helm 1954, Tryon 1954), sediments (Sculthorpe 1971, Barko et al. 1986), and water chemistry (Sculthorpe 1971, Barko et al. 1986). Since considerable speculation existed about the relative importance and mode of action associated with these and other factors responsible for recent declines of macrophytes, the Lake Michigan District of the Wisconsin Department of Natural Resources (WDNR) formed the Fox-Wolf Lakes Task Force in 1974. Their charge was to assemble baseline data on habitat deterioration, assess the impacts of habitat loss on fish and wildlife resources, and discuss problems associated with water level fluctuations and improved water level management. As part of the task force, the WDNR Bureau of Research initiated a study of macrophyte changes and associated limiting factors in 1974. The project ended in 1983. Specific objectives of this study were to: (1) document historical changes in the quantity and quality of macrophytes related to water level management, (2) determine the ecology, quantity, and quality of existing macrophytes, (3) identify factors affecting distribution and abundance of macrophytes, and (4) evaluate restoration techniques for macrophytes.

Due to the size and complexity of this ecosystem and the very modest level of funding for this project, these objectives could only be approached in a general manner during the 1975-82 study period. The first 2 objectives received the most attention. For the third objective, this study investigated relative impacts of water level fluctuations, water clarity, and exposure to waves and undesirable fish on macrophytes in the UWPL. Additionally, a serious insect infestation on round-stemmed bulrushes provided an opportunity to assess potential impacts of insects on macrophytes. For the fourth objective, this study investigated several methods of transplanting common reed rhizomes. This report summarizes the limited findings of the study and liberally interprets them through integration with information from an extensive literature review to develop management recommendations applicable to the UWPL, as well as other large shallow lakes in the Upper Midwest.

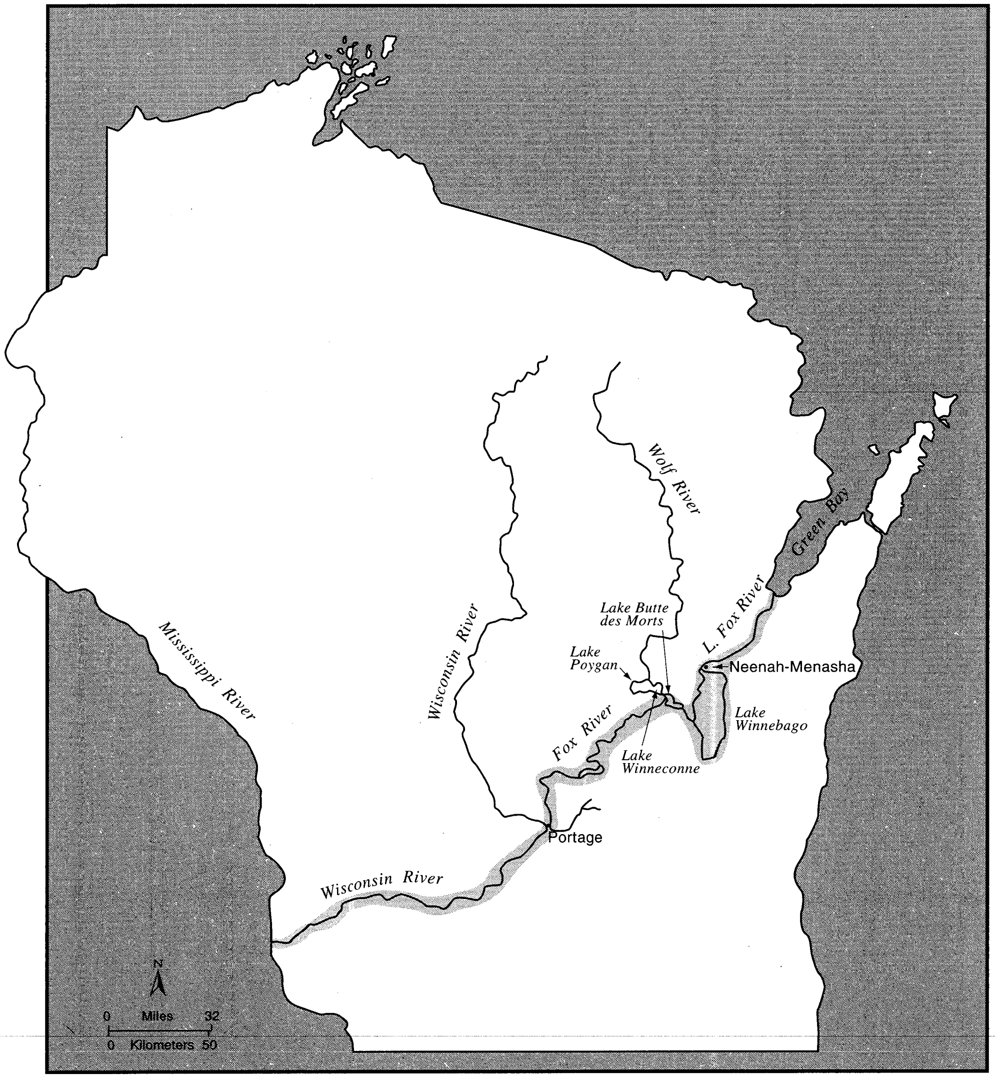


Figure 1. *Fox-Wisconsin Rivers waterway from Green Bay to the Mississippi River, which was used for commercial navigation during the late 1800s and early 1900s.*

STUDY AREA

Lakes Poygan, Winneconne, and Butte des Morts are part of the Lake Winnebago system located in east-central Wisconsin. This system is in the Lake Michigan drainage basin (Fig. 1). Presently, Lake Poygan covers 14,102 acres, Lake Winneconne 4,507 acres, and Lake Butte des Morts 9,234 acres (Fig. 2). These lakes reach maximum depths of about 11 ft, primarily in the old channels of the Wolf and Fox Rivers. Approximately 10% of the surface area has water depths of 3 ft or less (Fassbender and Nelson 1975). These lakes have relatively uniform shallow basins devoid of much structure. Sediments range from soft silt and organics in the deeper areas and in protected bays to firm sand in many shallower exposed areas. The UWPL are more eutrophic and turbid than most Wisconsin lakes (Lillie and Mason 1983). Turbidity consists primarily of phytoplankton, but also suspended materials from soil erosion, wave action, and carp (Sloey and Spangler 1977). Frequent summer algae blooms and Secchi disk transparencies < 3 ft reflect the eutrophic condition of these lakes (Fassbender and Nelson 1975; U.S. Environ. Prot. Agency 1974, 1975).

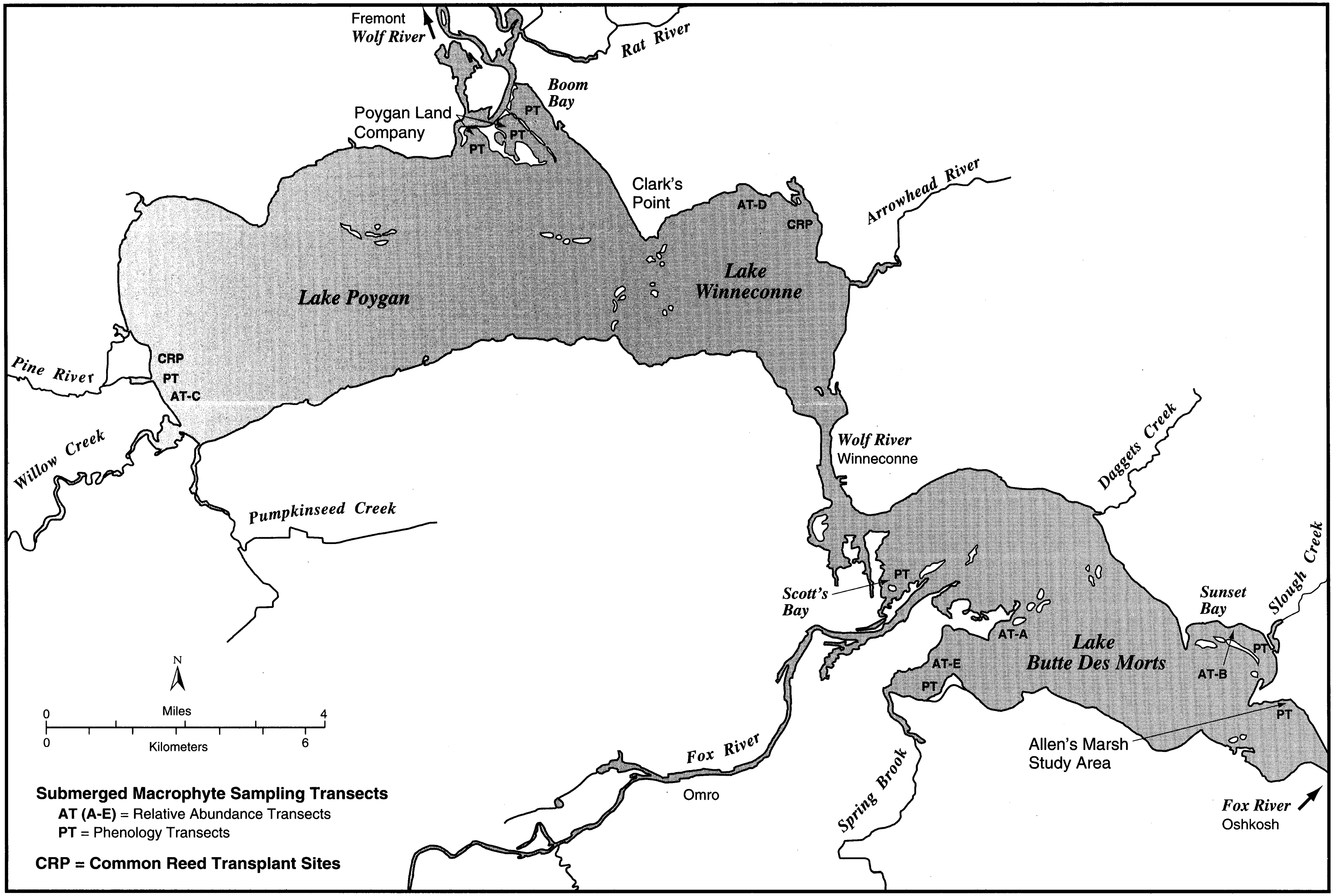


Figure 2. *Tributaries, study areas, and sampling sites on the Upper Winnebago Pool Lakes, 1975-82.*

METHODS

Review of Historical Records

Information on historical changes in macrophytes from the early 1800s through the early 1970s was assembled from written historical accounts, maps (especially U.S. Army Corps of Engineers and U.S. Geological Survey maps), photographs (especially U.S. Department of Agriculture, Agricultural Stabilization and Conservation Service high altitude aerial photos), and personal accounts of long-time residents. Major changes in macrophytes documented from these sources were then examined in relation to annual and seasonal water level changes (measured at the Oshkosh gage station) derived from daily water level records maintained by the U.S. Army Corps of Engineers since the late 1800s.

Documenting Ecology of Macrophytes

Distribution and abundance of emergent and submerged macrophytes during the study period were determined from low altitude (1,500-2,500 ft), vertical color photography in July-early September 1975-76 and 1978-79. Field surveys verified species composition and location, and monitored phenology, growth, and density during April-September 1975-82.

Phenology and growth rates of 5 emergent species were determined by sampling plants at irregular intervals during mid-April to early September 1976-82 at several locations to account for variability throughout the system. A maximum of 16 locations for wildrice, 8 for common reed, 12 for round-stemmed bulrushes (*Scirpus acutus* and *S. validus* combined due to difficulty distinguishing these species in the field), 4 for spike rush, and 14 for stiff arrowhead were monitored at various times during the study period. Beginning and ending dates for major phenological events represent 4-23 observation dates variously spread over the 7-year period. Typically, 10-20 stems (but ranging from 5-90 stems) were subjectively selected at representative sites within a stand of each species on each sampling date. Water depth and stem height above the sediment were measured and phenology (flowering, fruiting, senescence) noted. Although observer bias associated with subjective stem selection contributed an unknown amount of variability, these data provided a general description of growth patterns and phenology. Relationships between average height of mature stems measured in July-August 1981 and water depth among several different stands for 4 emergent species (common reed, round-stemmed bulrushes, spike rush, and stiff arrowhead) were analyzed with simple linear regression analysis (SAS Institute 1982).

Phenology, species composition, and relative abundance of submerged macrophytes were documented along transects in 8 areas of the UWPL (Fig. 2). Transects were sampled at irregular intervals from April-August of 1977 and 1979-82 and are referred to as "phenology" transects. For each area, data were pooled for all dates in May-June (3-16 dates over 1-5 years) and in July-August (4-12 dates over 1-4 years) to document species composition for early- vs. late-maturing species.

Along the phenology transects, submerged macrophytes were sampled 1-12 times during a growing season with a rake modified after Jessen and Lound (1962). While motoring at a constant speed along a subjectively selected course through each submerged macrophyte bed, 3-15 rake samples were obtained by dragging the rake behind the boat for 3-10 sec. Vegetation was sorted to species, and wet volumes were estimated for samples patted dry with paper towels to determine relative contribution of each species to total vegetation. Phenological status was determined for all stems apparently broken off near the sediment surface.

More specific information on timing of various phenological events of both submerged and emergent macrophytes was obtained from observations recorded in journals kept whenever field assistants visited the lakes.

Changes in abundance of submerged macrophytes were monitored annually from 1975-80 along 5 additional transects, referred to as "relative abundance" transects, in the UWPL (Fig. 2). The starting point and direction of transects were subjectively selected at the north shore of Lake Winneconne, the west shore of Lake Poygan, and in 3 bays of Lake Butte des Morts in 1975. Once each summer thereafter, transects were reestablished using a transit and identifiable landmarks. Abundance of submerged macrophytes was estimated for 100 points located at 53-ft intervals along 1-mile-long transects. At each point, samples were collected by dragging a rake the length of its handle along the bottom. Relative coverage (%) of the rake tines was estimated for each rake sample in all years, and in 1979-80, wet volumes also were determined as above. Chi-square tests examined differences in frequency of occurrence among years. Precision of estimating rake coverage was evaluated by comparing wet volume estimates for 5 classes of rake coverage (1-12%, 13-37%, 38-62%, 63-87%, and 88-100%) with 1-way Analysis of Variance (ANOVA), followed by Tukey's Studentized Range Test (TSRT).

A continuous recording thermograph monitored water temperature at a mid-column and a sediment-water interface point during the growing season at the Lake Poygan west shore site in 1976-77 and 1981, and at 2 sites in Lake Butte des Morts: Nickel's Marsh-west in 1976 and the Allen's Marsh Study Area (AMSA) in 1979 and 1981 (Fig. 3). Growth stage of several species was then related to water temperatures at these sites.

Water depth tolerances for 5 emergent species (wildrice, common reed, round-stemmed bulrushes, spike rush and stiff arrowhead) were derived from depths measured at

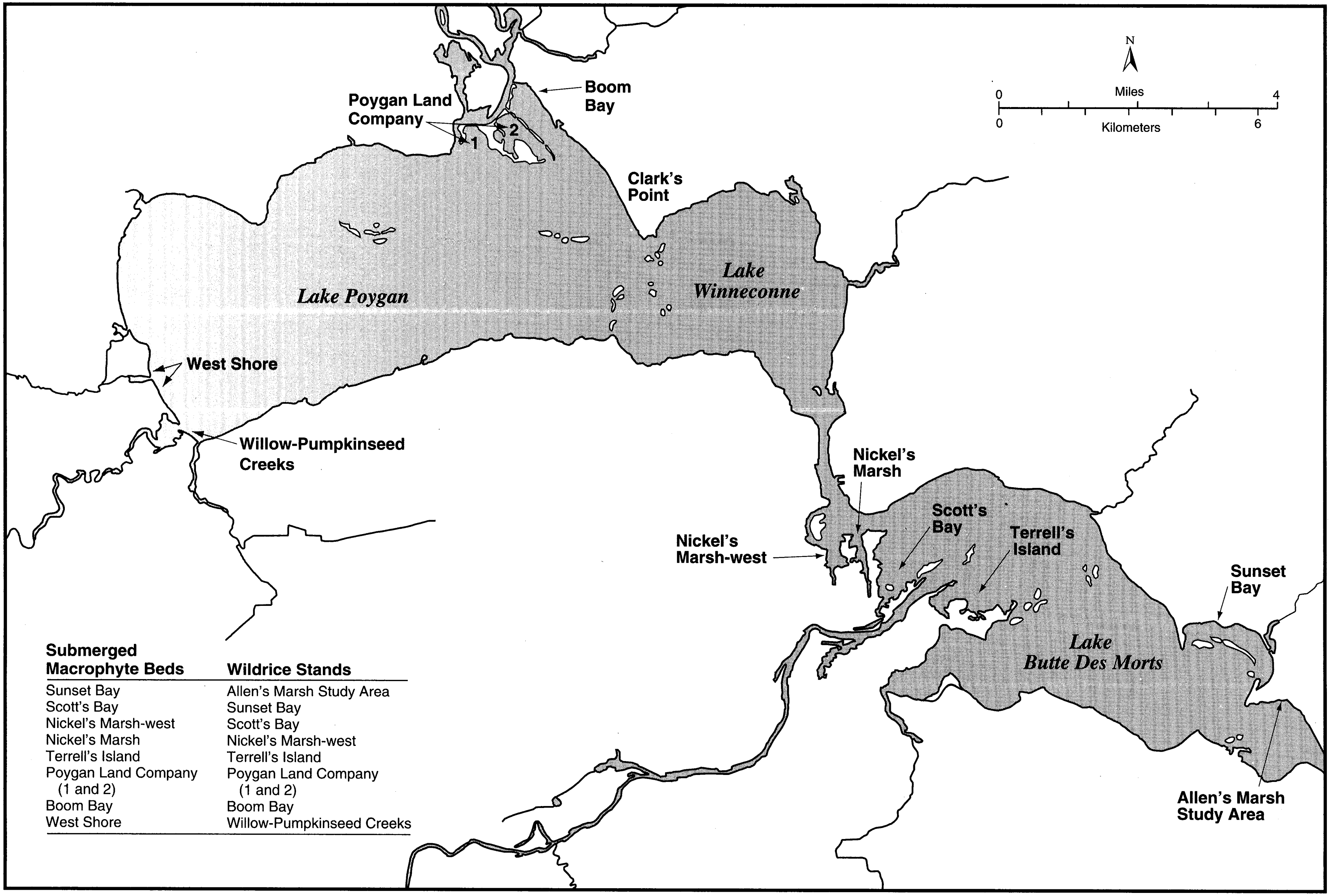


Figure 3. *Location of 8 wildrice stands and 8 submerged macrophyte beds in the Upper Winnebago Pool Lakes, 1975-82.*

the lakeward edge of plant beds at least once during summer, 1981. Water depth tolerances for submerged macrophytes were derived from measuring water depth at every 10th station along the relative abundance transects and at the outer margins of plant beds elsewhere during 1975-80. Differences between these water depth measurements and water level readings at Oshkosh yielded a correction factor to extrapolate maximum tolerances from mean monthly water levels in each month during spring and summer of that year. Water level data were averaged for 5 days surrounding the date of sampling, but severe outliers were eliminated as these likely reflected major seiche events. This extrapolation method also provided correction factors for comparison of monthly water depth tolerances of several species from August 1969 (Harriman 1970) to tolerances during this study.

Sediment types for 3 emergent species were determined by collecting 6-inch sediment cores at 21 sites from 2 stands of wildrice, 8 sites from 1 stand of common reed, and 19 sites from 2 stands of round-stemmed bulrushes. For submerged macrophytes, sediments were sampled at every 10th sampling point along the relative abundance transects in 1977. Feel, appearance, and color of moist samples provided subjective criteria for classification to major texture classes (sand, clay, silty-organic, or fibric).

Percent organic content of sediments was determined from changes in weight of samples oven-dried at 103 C to a constant weight, then ashed at 550 C for 1 hour. Fisher's Exact Test was used to analyze the relationship between frequency of plots with and without submerged macrophytes between the 2 most common texture classes, sand vs. silty-organic. Rake coverage of submerged macrophytes was compared between these 2 texture classes with *t*-tests employing the arcsine-square root transformation. *T*-tests employing the arcsine-square root transformation were also used to compare organic content for plots with vs. without submerged macrophytes and for sand vs. silty-organic texture classes.

Total nonstructural carbohydrate (TNC) content was determined for rhizomes of round-stemmed bulrushes collected during the growing season of 1978 from the AMSA (Fig. 3). For 12 sampling dates, 4-10 sections of 1-inch length were extracted from 2-5 rhizomes for analysis following techniques described in Smith (1969). Changes in TNC content were then related to phenological events and growth of round-stemmed bulrush stems sampled in 9-10 systematically located circular plots (6.9 or 6.4 ft^2) during 1978-81, and to all round-stemmed bulrush stems within a 625 ft^2 wave and carp exclosure in the same general area during 1976-77.

Evaluating Techniques for Common Reed Re-establishment

The feasibility of transplanting common reed rhizomes was evaluated by separating small clumps of rhizomes and shoots from established stands and transplanting them to the north shore of Lake Winneconne and the west shore of Lake Poygan (Fig. 2). Three planting techniques were evaluated for stabilizing sediment around the plantings: (1) sandbags containing sediment and rhizomes with stems protruding through holes placed in excavated depressions or on the sediment surface, and additional sandbags placed around the surface plantings; (2) burlap bags containing sediment and rhizomes placed inside old tires filled with sand; and (3) rhizomes buried in the sediment then covered by a piece of chicken wire with a hole in the center for protruding shoots, and held flush with the sediment surface by 7-inch wire staples.

Rhizomes were harvested and transplanted from late April to late June 1977-78. Some extracted rhizome clumps were stored for up to 10 days by anchoring them in the parent stand. Rhizomes planted in Lake Winneconne on 16 May 1978, however, were stored submersed in plastic pails in an unheated shed for 3 weeks. Rhizome clumps contained 1-50 green stems with a height varying from 0.2-5.0+ ft at harvest. Number and height of stems were monitored at irregular intervals throughout each growing season until the planting failed. For Lake Winneconne plantings, stem height was also measured in a nearby control plot of naturally established common reed. Planting site depth ranged from 0.2-2.0 ft at the Winneconne site and 2.0-3.0 ft at the Poygan site.

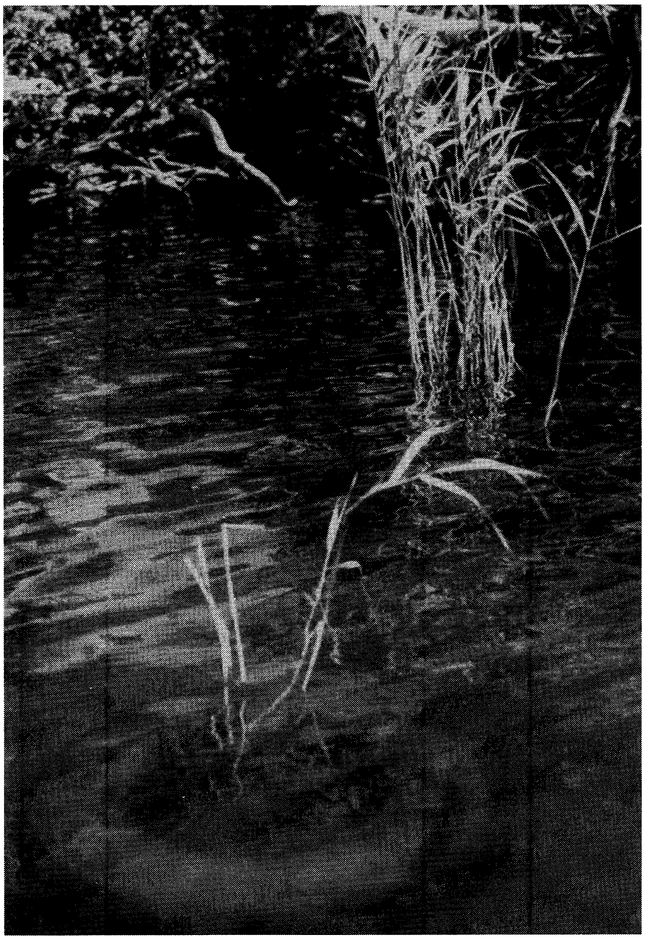
Assessing Factors Affecting Macrophyte Abundance

Water Levels

Daily water levels were obtained from a water level gage in Oshkosh operated by the Corps of Engineers. Differences in mean water levels among months and for each month among years were analyzed with 2-way ANOVA. TSRT was used to test differences among months for each year and among years for each month. The frequency of excessively high daily water levels among months and years was analyzed with Chi-square tests. Excessively high water levels were defined as days with levels greater than 3.0 ft at the Oshkosh gage. This was the target summer water level of a management plan implemented in 1982-83 to stabilize water levels and protect macrophytes (Append. A).

The short-term effects of varying water levels on abundance of macrophytes were assessed by comparing the abundance of submerged macrophytes and wildrice to water level differences among years. Annual changes in frequency of occurrence of submerged macrophytes along relative abundance transects were compared to annual differences in mean monthly water levels, frequency of high water levels in spring (May-Jun) and summer (Jul-Aug), and minimum winter levels using Spearman's rank correlation analysis. Combined effects of mean monthly water levels and turbidity vs. annual changes in rake coverage of submerged macrophytes were evaluated with multiple linear regression analysis. Spearman's rank correlation analysis assessed the relationship between annual abundance (acreage documented from aerial photography) of wildrice in the AMSA and annual differences in mean monthly water levels for 1975-79.

(a)



(c)

PHOTOS: A. LINDE

(b)

One of several methods evaluated for transplanting common reed involved (a) harvesting rhizome clumps, (b) placing them in burlap bags containing sediment, (c) then placing these inside old tires filled with sand.

Effectiveness of a water level management plan in modifying monthly and annual water level patterns was evaluated by comparing mean monthly water levels for 1975-81 (prior to plan implementation) and 1982-84 (during plan implementation) with Wilcoxon rank sums test.

Water Clarity

Mean monthly and annual differences in water clarity were evaluated for photic zone depths, turbidity, Secchi transparency, and suspended solids. Data for these parameters were analyzed to determine differences in mean monthly photic zone depth and turbidity among months, years, and lakes, relationships among water clarity parameters, sources of turbidity, and effects of annual variations in water clarity on macrophytes.

Sampling sites and sampling frequency varied considerably throughout the study. Therefore, comparisons of photic zone depths and turbidity among lakes and months for each lake were weighted by a daily mean for all sites sampled each day. Each daily mean was calculated from data for a variable number (1-4) of sampling sites from a total of 4 different sites for Lake Winneconne, 8 for Lake Poygan, and 11 for Lake Butte des Morts. Sampling sites were subjectively selected in all areas of macrophyte investigations shown on Figures 2 and 3, plus Terrell's Island and Nickel's Marsh areas of Lake Butte des Morts, Clark's Point area of Lake Winneconne, and the common reed stands in north-central and east-central Lake Poygan. Analysis of differences in mean monthly photic zone depths and turbidity among months, years, and lakes utilized a factorial model ANOVA, followed by TSRT or *t*-test for differences among lakes by month.

Photic zones were defined for this study as the depth at which 95% of surface light has been attenuated by reflection and absorption of water and dissolved and suspended constituents. Thus, only 5% of surface light remained at this depth. Light penetration was measured with a Montedoro-Whitney light meter (sensitive to light in the 380-720 nm range) at 2-inch increments through the water column. The depth of 5% light penetration was then estimated from linear regression equations for each sample site and date. The regression model used a log transformation for percent light (0% penetration points deleted because of the undefined log transformation for 0) and an intercept of 0. This relationship is based on the equation:

$$\log_e(\%/100) = -nz$$

where:
$\%$ = percent light penetration at depth z,
$-n$ = slope of regression equation, and
z = depth.

This equation was derived from the formula for calculating the light extinction coefficient in pure water (Wetzel 1975). Several other transformations also were evaluated ($\log_e$-$\log_e$, inverse-inverse, square root-square root). Turbidity was measured with a Hach Model DR Colorimeter.

Linear regression analysis was used to examine relationships among water clarity parameters (5% photic zone, turbidity, and Secchi transparency) for several transformations, including inverse-untransformed, inverse-inverse, $\log_{10}$-untransformed, and $\log_{10}$-$\log_{10}$ (Lillie and Mason 1983).

Turbidity measured at the mouths of lesser tributaries, at major inlets and outlets, and at various in-lake sites of Lakes Poygan and Butte des Morts was compared among these potential sources. Turbidity was sampled irregularly from April-July 1975-78 and 1981 at the mouths of 6 tributaries (Pine River and Willow and Pumpkinseed creeks for Lake Poygan; Spring Brook and Dagett's and Slough creeks for Lake Butte des Morts; Fig. 2). Mean monthly turbidity for these tributaries was derived from weighted daily means for a variable number of tributary sampling sites (1-3) per day, and a variable number of sampling dates (1-6) per month. Also, turbidity and suspended solids were sampled weekly near the major inlets and outlets of the Wolf River at Fremont and Winneconne and the Fox River at Omro and Oshkosh, from May-August 1975 and during April 1976 (Fig. 2). Analysis of water samples for total suspended solids (TSS) and organic suspended solids (OSS) followed standard methods (American Public Health Association et al. 1971), except filters and non-filterable residue were ashed at 450 C for 6 hours instead of 550 C for 1 hour.

Water clarity differences were tested among months using pooled data for all lesser tributaries, and among lesser tributaries using pooled data over all months by 1-way ANOVA and TSRT. Sample sizes were too variable and small to test differences among tributaries by month or among months by tributary. Differences among major inlets and outlets and among months for turbidity, TSS, and OSS were assessed with a factorial model ANOVA, followed by TSRT.

For Lakes Poygan and Butte des Morts separately, mean monthly turbidity was compared among major inlets, major outlets, all in-lake sites pooled, and all lesser tributaries pooled for each lake for May-August 1975 and April 1976 using 1-way ANOVA and TSRT . This subset included data from various sites (1-3) per day and days (1-5) per month for each source.

Spearman's rank correlation analysis examined relationships between annual frequency of occurrence of submerged macrophytes along relative abundance transects B and C and annual turbidity and photic zone depth for spring (Apr-Jun) and summer (Jul-Aug) of the same and the previous year. Water clarity data for this analysis utilized the weighted daily means calculated from all in-lake sites sampled each day and used in the analysis of water clarity differences among lakes and months.

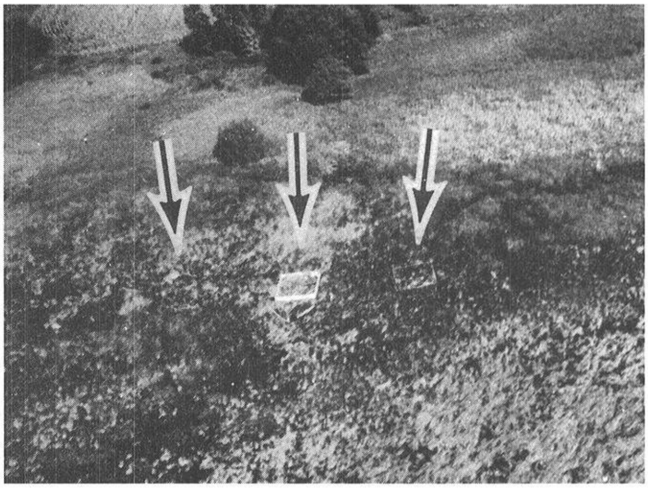
Impacts of Waves and Undesirable Fish

The contribution of suspended sediments to water turbidity by wind-generated wave action was assessed by comparing daily wind speeds to in-lake turbidity and photic zone depths. Wind speed and direction data for every half hour during April-September 1977-82 were obtained from the Oshkosh Municipal Airport, located approximately 4 miles southeast of Lake Butte des Morts. For each day, the prevalent wind direction, mean wind speed, maximum wind speed, and maximum gust speed were determined. Gusts were defined as infrequent and atypically strong winds compared to average wind speed measured throughout the day. One-way ANOVA and TSRT distinguished differences among mean monthly wind speeds for data pooled over all years.

Simple linear regressions assessed relationships between mean daily turbidity and photic zone depth vs. mean daily wind speed, mean daily wind speed incorporating gusts, mean daily gust speed, and maximum daily wind speed. These comparisons incorporated all water clarity sampling days from April to August and used mean turbidity and photic zone depths calculated from all in-lake sites sampled each day (1-4 sites). Additionally, mean daily turbidity and photic zone depth were regressed on mean daily wind speed in April-May only. Using only spring data reduced the confounding effect of frequent phytoplankton blooms and sampling bias in vegetated areas during summer. Lastly, mean daily turbidity and photic zone depth for sites in western Lake Poygan and sites in the Sunset Bay area of Lake Butte des Morts were regressed on mean daily wind speed for days with onshore winds. These were the only nearshore sites with adequate sampling days to assess the impact of waves over long fetches.

Water clarity differences associated with wave attenuation by macrophytes allowed further examination of the relationship between wave action and water clarity. Turbidity was measured at irregular intervals from April-September at 3 sites: a submerged macrophyte bed at Lake Poygan's west shore during 1976-77 (1-7 sampling dates per month), a mixed wildrice-submerged macrophyte stand at the AMSA during 1978-79 (1-3 sampling dates per month), and a common reed stand in Sunset Bay during 1975-76 (1-5 sampling dates per month). At each site, turbidity was measured at the shoreward margin of macrophytes, the interior of the stand, and beyond the lakeward margin of macrophytes. TSS and OSS were also measured for the 3 common reed sites. Differences among sites and among sampling dates were analyzed with 2-way ANOVA, followed by 1-way ANOVA and TSRT of sampling site differences in each month.

Direct physical impacts of waves and carp on macrophytes were investigated from 1975-80 with an exclosure experiment incorporating 2 protection treatments and a control plot at the AMSA (Fig. 2). Exclosures were 25 ft by 25 ft in size. Theoretically, a solid panel structure excluded both waves and carp, whereas a wire structure excluded only carp. The original experimental design involved sets of these plots at 5 different locations in the UWPL in 1975, but waves and ice severely damaged structures at all locations except the AMSA during 1975-76. Treatment and control plots at this site were subjectively located in a littoral zone surrounded by a heterogeneous mix of emergent and submerged macrophytes. In April 1979, both exclosure structures were removed and plots permanently marked for subsequent sampling in 1979-80. Water depths were similar among all 3 plots, but ranged from 16-30 inches during the study.



A solid panel wave barrier (middle), a wire mesh carp exclosure (right), and a control plot (located equidistant to the left of the solid panel exclosure) tested the direct physical impacts of waves and carp on macrophytes in the Allen's Marsh Study Area of Lake Butte des Morts.

PHOTO A. LINDE

For each plot, macrophytes were sampled at 20 systematically located points by harvesting all vegetation in a 0.67-ft^2 area during late July through mid-August 1975-80. The wire mesh exclosure was not sampled in 1975-76 and 1980, and emergent macrophytes were not sampled in any plot in 1976. Sorting samples to species and drying for 4 hours at 75 C yielded dry weight biomasses. Differences among treatments and years for total biomass of macrophytes were determined with a factorial model ANOVA. A differential response by emergent vs. submerged macrophytes led to a second, separate analysis of each group using a factorial model ANOVA. Finally, TSRT examined differences among years by treatment and among treatments by year for the 2 macrophyte types.

Insect Infestations in Round-stemmed Bulrushes

Premature discoloration, death, and loss of stems within the solid-panel exclosure in 1977 prompted closer scrutiny of insect damage in the AMSA during 1977-80. Green and discolored stems were subjectively collected on 3 days in July-August 1977 (48 stems) and 11-12 days in early June-early September 1978 and 1979 (225 and 261 stems, respectively). Each stem was split open and checked for boring insects and signs of insect damage. William H. Hilsenhoff (University of Wisconsin-Madison) initially identified several larvae and pupae used as references for future identification. Variations in stem density and phenology of stems sampled during 1977-80 in 9-10 systematically located plots (6.9 ft^2 and 6.4 ft^2 circular plots for 1977 and 1978-80, respectively) were then related to insect infestation rates. Plots were spaced 10 ft apart along a transect perpendicular to the shoreline with the first plot located about 10 ft inside the shoreward edge of a bulrush stand. One-way ANOVA evaluated differences in stem density among sampling dates within a year and among years for similar sampling dates.

RESULTS AND DISCUSSION

History of Macrophyte Changes and Water Level Management

Prior to impoundment in the 1850s, the UWPL were naturally eutrophic, large riverine marshes supporting dense emergent macrophytes dominated by wildrice (Linde 1979). Large sedge meadows and lowland prairies surrounded the marshes. Fish and wildlife populations thrived in these optimal habitats.

Settlement and fur trading on the Lower Fox River in the late 1700s through the early 1800s produced a strong demand for transportation routes (Linde 1979). One such waterway extended from lower Green Bay upstream on the Fox River to Portage, then across land and water via a canal to the Wisconsin River, and finally down to the Mississippi River (Fig. 1). This route required locks and dams throughout the Fox River system and a canal at Portage. Power generation was a secondary consideration (Linde 1979). Dams built in the 1850s on the Fox River at the Neenah and Menasha outlets on the north end of Lake Winnebago created the Winnebago Pool consisting of Lakes Winnebago, Butte des Morts, Winneconne, and Poygan (Fig. 1).

Major changes in species composition, abundance, and distribution of macrophytes occurred from the 1850s to the 1960s. The transition of the UWPL from a riverine marsh ecosystem to a large, turbid, open-water lake system encompassed 3 phases: (1) formation and disintegration of floating bog after impoundment from the 1850s to the 1920s; (2) replacement of bog by other emergents and submerged macrophytes from the 1930s to the 1950s; and (3) disappearance of these successional macrophytes in the 1960s.

1850 to 1930

The first major transition in macrophytes occurred from the 1850s to the 1920s and resulted primarily from increased water levels and extreme water level fluctuations after impoundment, especially in years of severe flooding (Linde 1979). Impoundment of the Winnebago Pool increased summer water levels by an average of 2 ft

1941

Extensive riparian marshes and shallow littoral areas supported dense beds of macrophytes in the Terrell's Island area of west-central Lake Butte des Morts (see Fig. 3) during the early 1940s. These marshy areas formed and constricted the Fox River channel and directed it far out into the lake. Most of these marshy areas declined or disappeared over the next 30 years, leaving a large, turbid open-water lake by the 1970s. This series of aerial photos shows changes from 1941 to 1971.

(Photos continued on pages 12-13.)

PHOTO: U.S. AGRICULTURAL STABILIZATION AND CONSERVATION SERVICE

(Photos continued from page 11.)

1950

1957

1964

1971

PHOTOS: U.S. AGRICULTURAL STABILIZATION AND CONSERVATION SERVICE

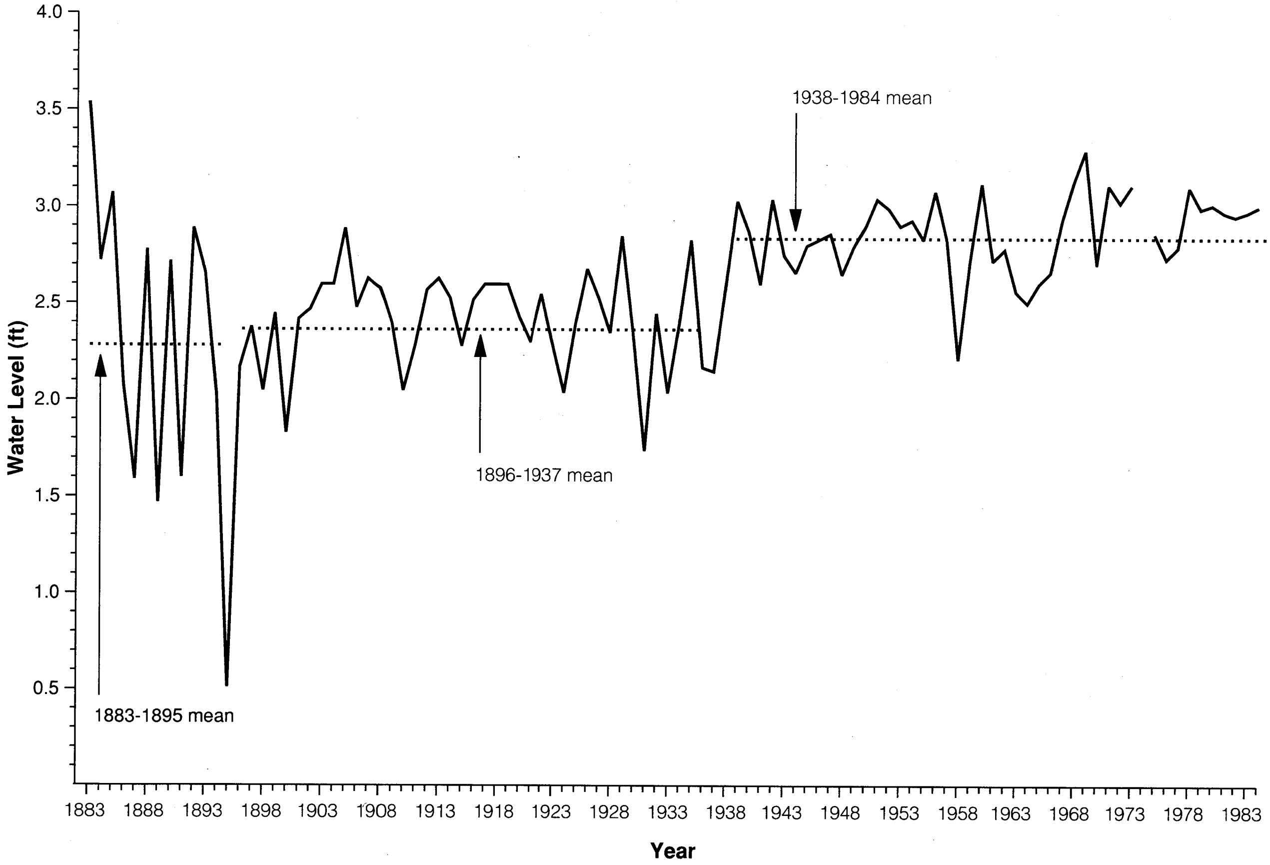
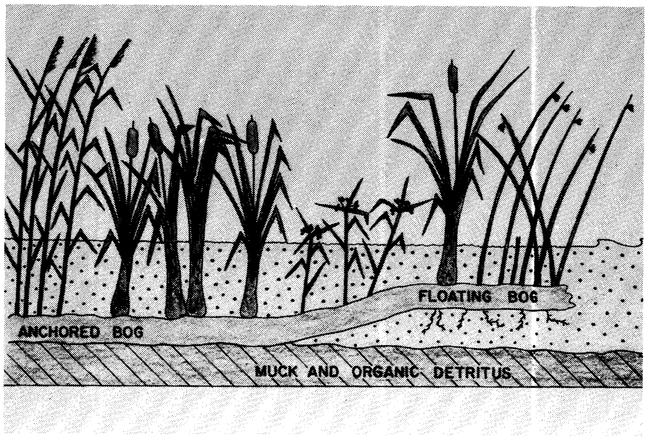
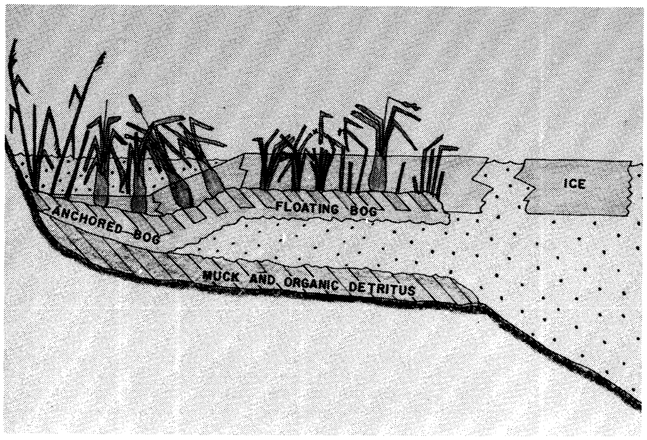


Figure 4. *Long-term changes from natural stage and annual fluctuations in mean late-spring and summer (May-Aug) water levels of the Winnebago Pool Lakes as measured at Oshkosh, 1883-1984 (modified from Linde 1975).*



Floating bogs are created when (a) high and fluctuating water levels lift dense rhizomatous mats away from underlying substrates;



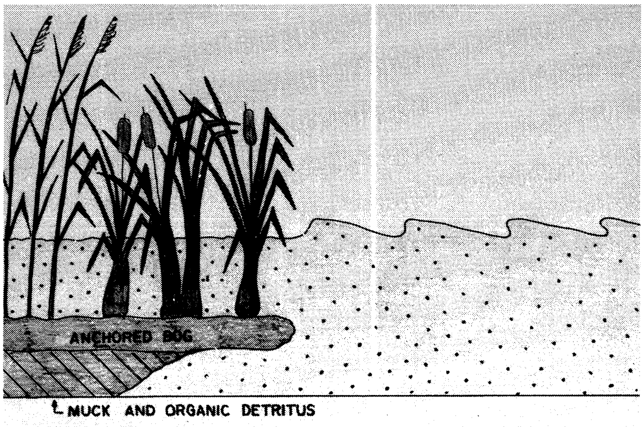
(b) rising water levels in spring prior to ice-out lift the ice layer formed within rhizomatous mats, tearing them away from bottom substrates;

in the 1850s, and subsequent modifications and improvements raised summer water levels an additional 0.5 ft in 1937-38 (Fig. 4) (Linde 1979). The resulting high water levels flooded thousands of acres of lowland marsh, sedge meadow, and prairie. Human development of land surrounding this large reservoir and diminished storage capacity of marshes for spring run-off necessitated water level management for flood control in the early 1900s. High water levels were maintained during late spring and throughout summer for navigation and power generation. A gradual drawdown beginning in October or early November (the end of the navigation season) provided storage capacity for spring run-off and augmented flow for power generation during the low-flow winter period. During spring runoff, water levels increased rapidly, and often rose uncontrollably prior to ice-out due to inadequate outflow capacity, insufficient reservoir storage capacity, increasing quantity and rapidity of runoff with watershed development and destruction of wetlands, and slow response to major runoff and precipitation events. Severe flooding and ice damage often ensued. Late spring and summer water levels fluctuated widely among years for these same reasons (Fig. 4).

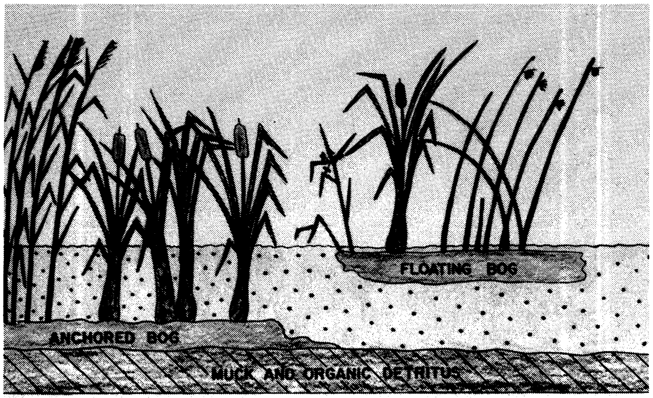
The 2.0-ft rise in water levels in the 1850s apparently eliminated emergent macrophytes from the deepest areas and created large expanses of floating bog consisting of wet meadow, lowland prairie, and emergent marsh macrophytes (Linde 1979). Bog formation likely occurred through several mechanisms: (1) buoyancy of dense rhizomatous mats due to excessive accumulation of gases from premature senescence of stressed plants and anaerobic decomposition; (2) lifting of ice layers frozen into the mats when water levels rose before ice-out in spring (Penko 1985); and (3) erosion of soft, unstable sediment from beneath rhizomatous mats by wave action and ice scour. Wave and ice action later disintegrated floating bogs and created small, floating islands of emergent macrophytes that severe flooding readily swept away. As floating bogs and emergent macrophytes declined, the area of open water expanded, allowing greater wave action that further exacerbated the problem (Linde 1979).

Total bog and marsh loss prior to 1961 approximated 5,200 acres on Lake Poygan, 1,500 acres on Lake Winneconne, and 3,800 acres on Lake Butte des Morts (Figs. 5 and 6). Most of the bog and marsh disappeared prior to 1937, with the greatest losses occurring in years with exceptionally high spring-summer water levels (Linde 1979). In 1881, water levels were 2.0 ft above the legal maximum water level or 3.0 ft above normal summer levels; in 1922, water levels were 1.3 ft above the legal maximum or 2.4 ft above normal summer levels as measured at the Oshkosh gage (Fig. 7).

As floating bog and emergent macrophytes disappeared, wave action and ice-scour eroded unstable organic sediments formerly held in place by dense root systems (McKee and Laudon 1972). This created deeper water areas, further limiting re-colonization by emergent macrophytes. From 1918 to 1968, water depths increased as much as 3 ft over most of the western half of Lake Butte des Morts in areas formerly occupied by emergent macrophytes (Fig. 8). Re-distribution of sediments probably continued through a second major loss of macrophytes in the UWPL during the 1960s.



(c) substrates under rhizomatous mats are scoured away.



(d) Wave and ice action then break these bogs into small islands that float downstream (illustrations by Arlyn Linde and Tom Janisch).

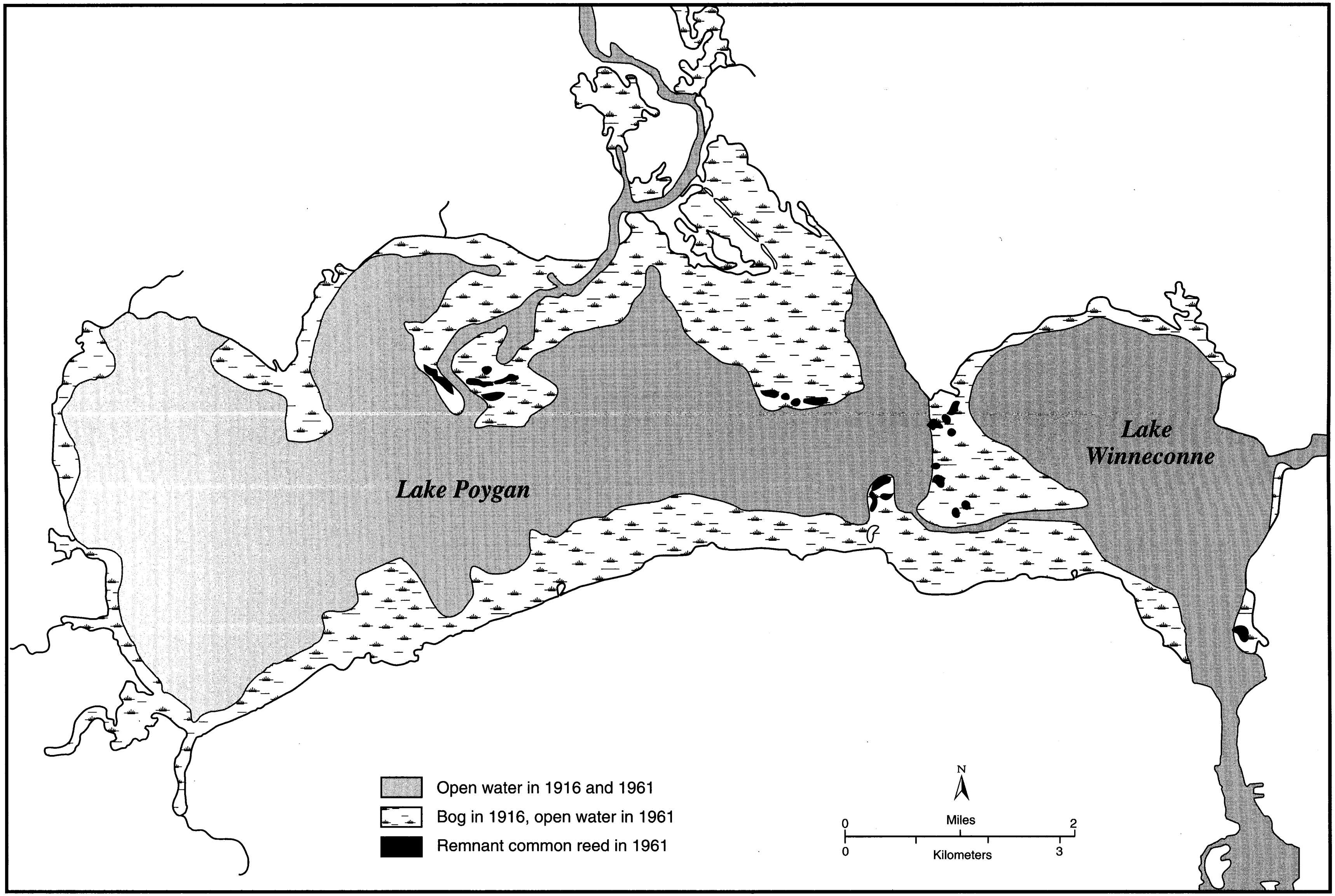


Figure 5. *Bog losses on Lakes Poygan and Winneconne, between 1916 and 1961 (modified from Linde 1975).*

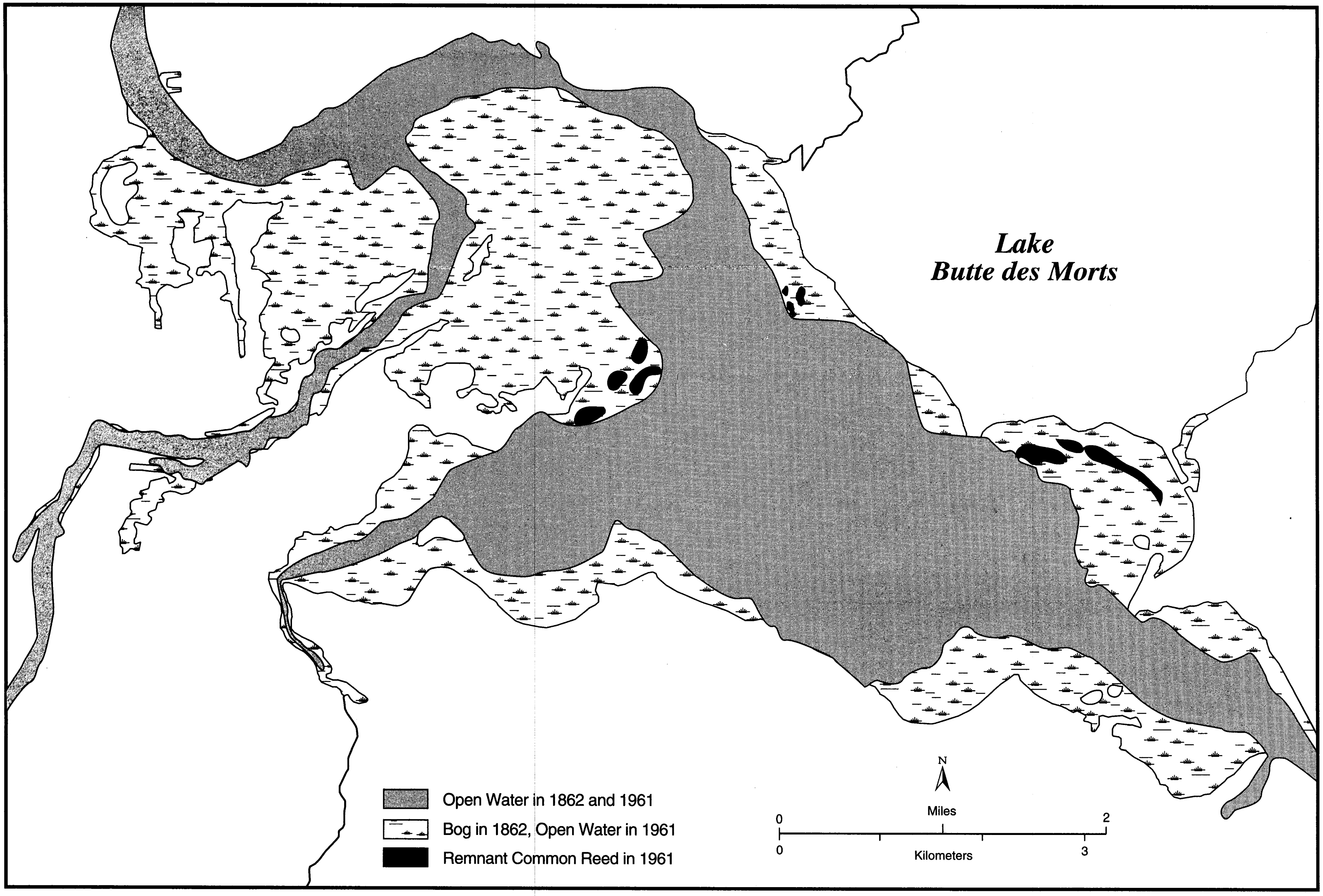


Figure 6. *Bog losses on Lake Butte des Morts, between 1862 and 1961 (modified from Linde 1975).*

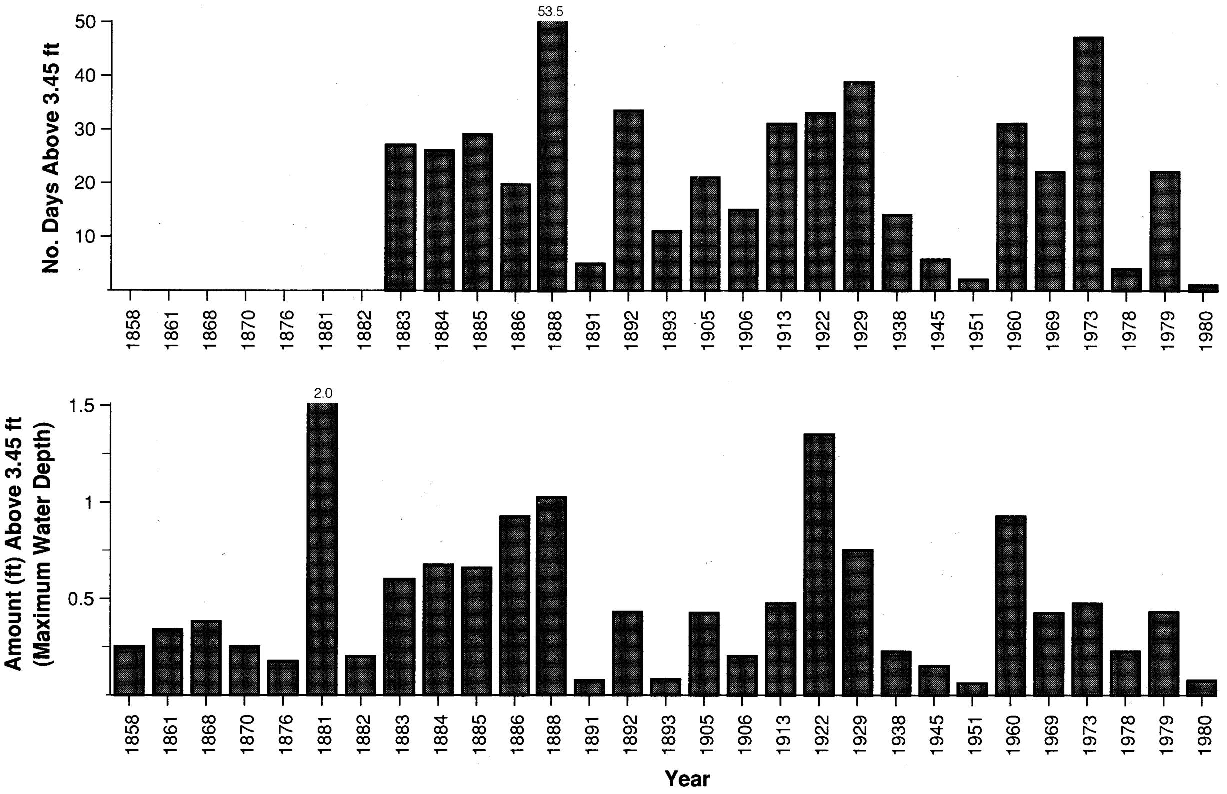


Figure 7. *Frequency and magnitude of water levels above the legal maximum of 3.45 ft at Oshkosh for the Winnebago Pool Lakes, 1858-1980 (includes only years in which water levels exceeded 3.45 ft) (modified from Linde 1979).*

1930 to 1960

Less drastic changes in water levels, water depths, and abundance of macrophytes marked the second transitional phase in macrophytes from the 1930s through the 1950s. Water level management shifted from commercial navigation to water storage for municipal and industrial use, waste dilution, and power generation. Commercial navigation had ceased by the 1940s (Linde 1979). Other goals included flood control and an emerging emphasis on recreation. This did not alter the general water level pattern seasonally.

Although late-spring and summer water levels continued to fluctuate annually, the long-term average increased by only 0.5 ft during this period (Fig. 4) (Linde 1979). Excessive flooding during late spring and summer occurred infrequently during this period with the worst flooding in 1960 (Figs. 4 and 7). This flooding and continued high water levels above the pre-impoundment stage during the 1930-60 period, coupled with the 0.5 ft increase in 1937, led to more bog formation and disintegration. Wave action and flooding apparently continued to erode and re-deposit large shoal and delta areas in the western half of Lake Butte des Morts and in northern Lake Poygan. Remnant stands of common reed in these areas mark the historical marsh and shoal boundaries (Figs. 5 and 6).

These water level fluctuations and depth changes from the late 1930s to late 1950s altered species composition and abundance of macrophytes. In the early 1900s, submerged macrophytes probably colonized the optimum habitat created in deeper areas by loss of competition and shading from floating bog and emergent macrophytes. Wildrice, round-stemmed bulrushes, river bulrush, and arrowheads (mainly stiff arrowhead) likely colonized shallow zones. In 1940-43, Lakes Winneconne and Poygan supported a greater profusion and diversity of macrophytes than most other large wetlands in Wisconsin with the exception of the Upper Mississippi River; but carp and fluctuating water levels, especially winter drawdown, had already contributed to a noticeable decline (Zimmerman 1953). Submerged macrophytes and deep-water species of emergent macrophytes slowly declined through the 1950s. This decline probably was due to stress from long-term high water levels and excessive seasonal fluctuations over previous decades, slowly increasing water depths from continuous erosion of sediments in littoral zones, and slowly increasing turbidity.

1960 to 1973

Water level management in the 1960s and 1970s followed the annual cycle dictated by management goals in the 1930-60 period. Average late-spring and summer water levels did not differ in the 1960s and 1970s from levels in the 1940s and 1950s. However, an accelerated decline in macrophytes in the early to mid-1960s created the large, turbid, open-water lakes evident during this study (Sloey

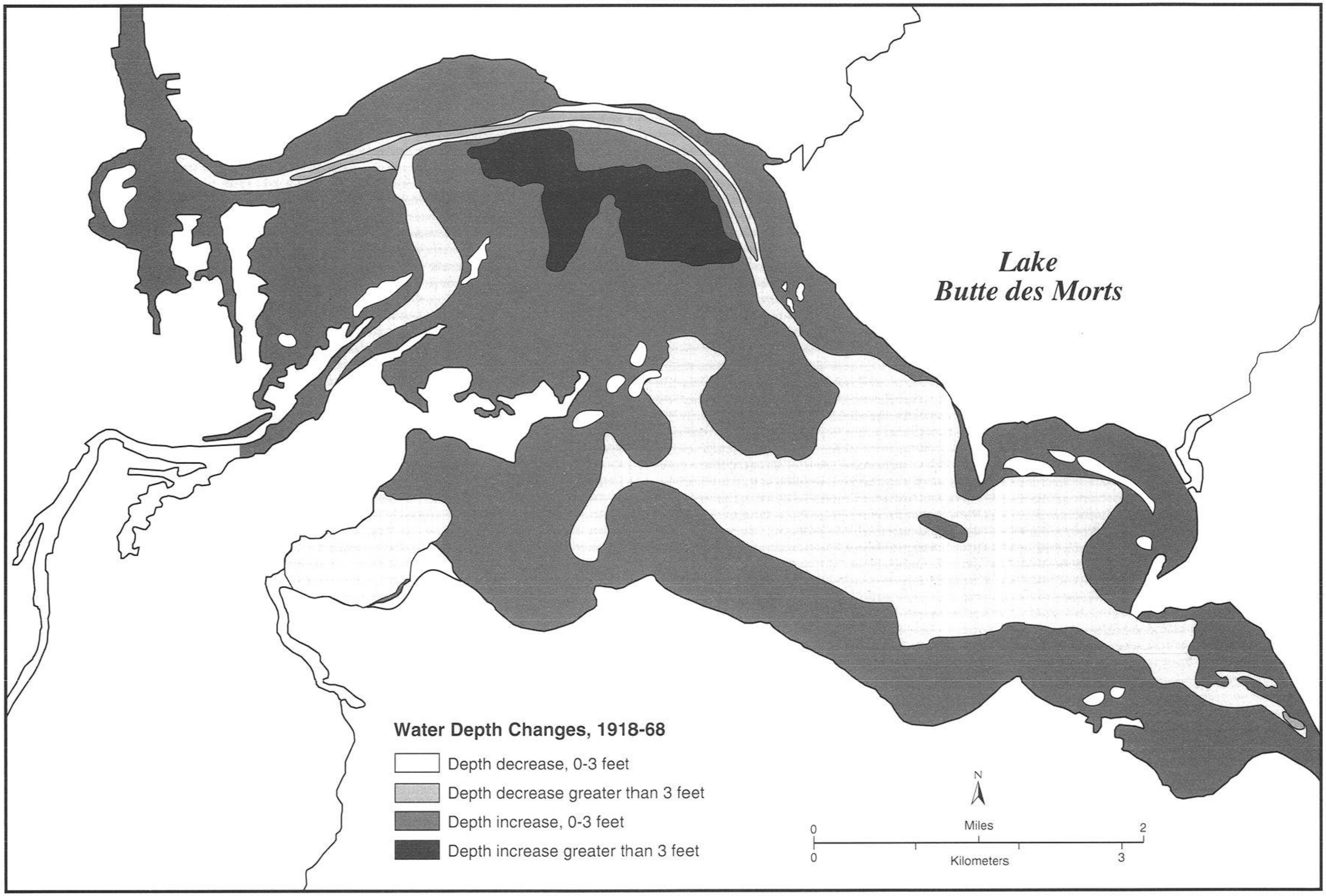


Figure 8. *Water depth changes occurring after bog loss and decline of macrophytes in Lake Butte des Morts from 1918-68 (from McKee and Laudon 1972).*

1970). This decline probably was influenced by extreme flooding and water turbidity, especially resulting from nutrient loading from municipal waste water, agricultural lands, unstable shorelines, lake shore developments, carp and freshwater drum, and wave action. In particular, severe flooding in late spring and summer of 1960 resulted in higher water levels (1.6 ft above normal) that persisted longer (31 days) than in any year since 1922 and 1929 (Fig. 7). Furthermore, high turbidity from nonpoint sources and erosion of previously unexposed shorelines likely accompanied flooding. These conditions could have greatly reduced the photic zone during May-June, eliminating macrophytes from all but the shallowest and most protected areas. Turbid floodwaters during 1943-44 in Lake Chautauqua along the Illinois River (Mills et al. 1966) and during 1978 in Pool 8 along the Upper Mississippi River (C. Korschgen, U.S. Fish and Wildl. Serv., pers. comm.) probably caused a decline of submerged macrophytes in these areas.

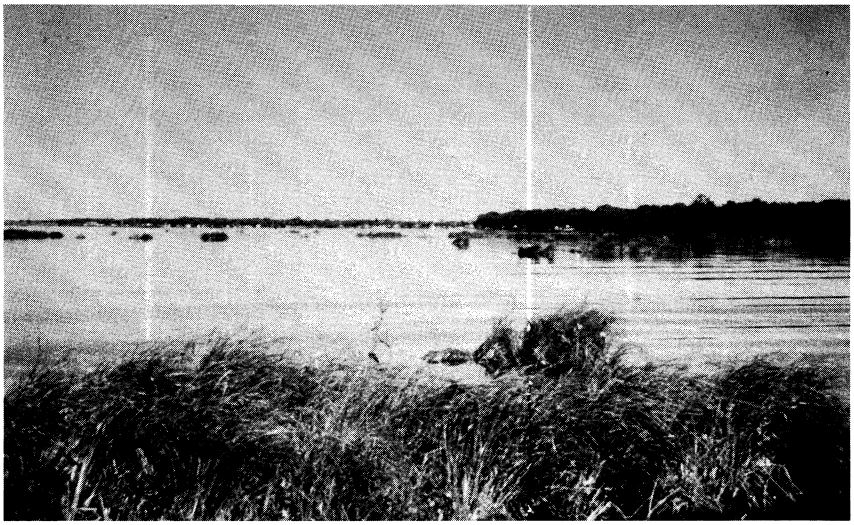
After loss of macrophytes in the 1960s, high turbidity prevailed. Plant growth no longer stabilized bottom sediments, dissipated wave action, and competed with phytoplankton for nutrients. Finally, severe flooding of long duration occurred again in 1969 and 1973 (Fig. 7), which probably further reduced the abundance of macrophytes. A noticeable disintegration and loss of floating bog from adjacent marsh habitat accompanied a severe wind storm in 1968 and excessive flooding in spring and early summer of 1969 (Sloey 1970).

Flooding of greater magnitude than in any year since 1929 occurred 3 times within 14 years from 1960-73. However, high water in most years apparently created and eroded more floating bog (McKee and Laudon 1972); but marsh and bog loss occurred more slowly and therefore was not very noticeable.

As macrophytes disappeared in the UWPL, wildlife populations declined. Predator fish populations presumably also declined due to decreased habitat, reproductive success, foraging efficiency, and food resources. Their reduction could have allowed carp and freshwater drum populations to expand, adding to turbidity and macrophyte loss. Trawling and boom-shocking in 1974-75 indicated that freshwater drum and carp comprised 67-68% of the total fish biomass collected in Lakes Butte des Morts and Poygan (Weber 1975).

Fall duck use declined noticeably during this period (G. Jolin, unpubl. data). Peak fall duck populations ranged from 108,500 in 1956 to 15,000 in 1962, but rebounded to 45,000 in 1964 and 1965 (Fig. 9). Censuses were discontinued until 1968-69 when a maximum of only 2,200 ducks were counted in both years. Continental breeding populations of ducks (pooled for 10 common species) also declined in the early 1960s and remained low through the mid-1960s (U.S. Fish Wildl. Serv. 1985) in response to severe drought conditions on the breeding grounds (Fig. 9). Unlike migrational populations on the Winnebago Pool Lakes, continental breeding populations rebounded in the late 1960s and early 1970s. Furthermore, migrational populations on the Winnebago Pool Lakes declined considerably more than continental breeding populations during the mid-1960s.

Despite extreme flooding in 1960 that possibly decimated macrophytes, populations of migrating waterfowl did not decline until the mid-1960s. A strong migratory instinct may have delayed waterfowl avoidance of these lakes after habitat deteriorated. Canvasbacks comprised the majority of ducks using these lakes in the late 1950s and early 1960s. Strong site fidelity of canvasbacks during migration could explain continued canvasback use of the UWPL for several years after loss of macrophytes, especially wildcelery and sago pondweed, both important foods. Perhaps macrobenthos (an alternative food source) remained abundant for several years after the macrophyte decline (see Kahl 1991), although macrobenthos densities were low in these lakes during 1990-91 (R. Kahl, unpubl. data). After a major decline in wildcelery on many pools of the Upper Mississippi River during 1988, peak populations of canvasbacks also decreased significantly, but relatively large numbers of canvasbacks continued to visit these pools during 1989-90 in spite of low food availability (C.E. Korschgen, U.S. Fish and Wildl. Serv., pers. comm.)



Disintegration and loss of large sections of floating bog caused by severe flooding occurred as recently as 1969 on Lake Butte des Morts.

PHOTO: W. SLOEY

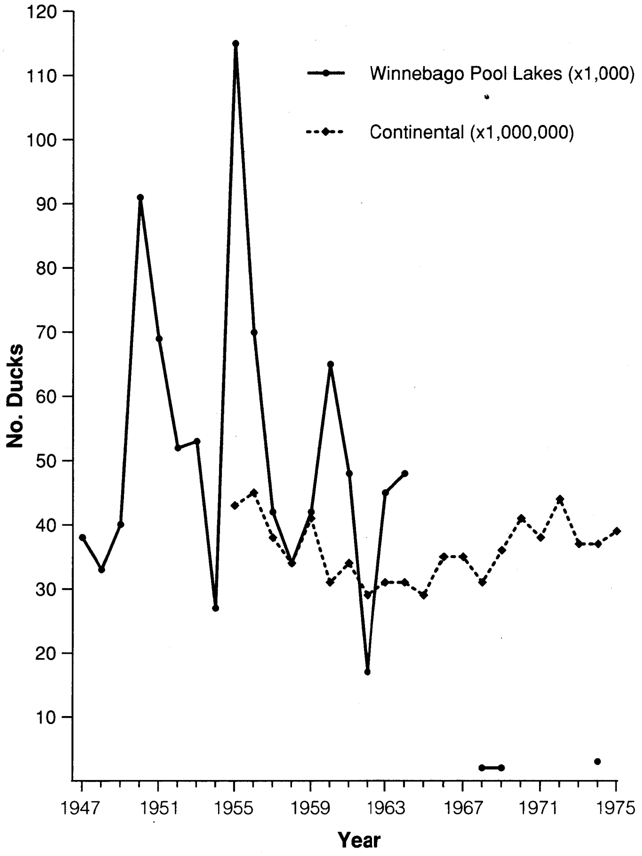


Figure 9. *Peak fall populations of all species of ducks on the Winnebago Pool Lakes, 1947-74 (determined by 1-5 aerial censuses each fall; from G. Jolin, Wis. Dep. Nat. Resour., Oshkosh, unpubl. data), and continental breeding populations pooled for 10 common species of ducks, 1955-75 (U.S. Fish and Wildl. Serv. 1985).*

Ecology of Macrophytes

Wildrice

Distribution and Abundance. During 1975-79, Lakes Butte des Morts and Poygan supported relatively large stands of wildrice at 8 sites (Fig. 3). There were approximately 475 acres of wildrice of mostly sparse to moderate density at these locations in 1976 and 350 acres in 1978 (Table 1). Sparse stands of wildrice also occurred in most shallow-bay and adjacent marsh-edge habitats. The Poygan Land Company and Boom Bay areas of Lake Poygan, and the Nickel's Marsh and Scott's Bay areas of Lake Butte des Morts supported the largest stands in 1976 and 1978.

Wildrice apparently was more abundant at lake sites during 1974-79 than in 1969. In August 1969 wildrice was widely distributed in the UWPL, but the stands were small (Harriman 1970). Adjacent marshes supported larger populations of wildrice. Prolonged, severe flooding in May and June 1969 (Fig. 7) could have eliminated or reduced the density of wildrice at most sites.

Wildrice nearly disappeared during the summer of 1984 at lake sites that had abundant wildrice during 1976-82; these sites supported little or no wildrice in 1985 (A. Techlow, Wis. Dep. Nat. Resources, pers. comm.). Several severe thunderstorms with strong winds and heavy rainfall that increased water levels 0.5 ft from 9 to 21 June 1984 may have stressed or uprooted plants. Wildrice cannot tolerate water level increases greater than 0.5 ft, especially during the floating-leaf stage (Moyle and Hotchkiss 1945). Their shallow roots are susceptible to uprooting, particularly when their floating leaves are pulled upward by rising water (Stoddard 1960)

Table 1. *Acreage of wildrice for 8 locations in Lakes Butte des Morts and Poygan determined from aerial photography in July to early September, 1975-76 and 1978-79.*

	Acreage by Year*			
Location	**1975**	**1976**	**1978**	**1979**
Lake Butte des Morts				
Allen's Marsh	6.8	16.6	35.9	35.8**
Sunset Bay	–	35.4	38.4	35.8
Scott's Bay	–	116.2	39.8	42.7
Nickel's Marsh-west	–	135.00**	23.0**	–
Terrell's Island	–	–	39.0	–
Total	–	303.2	176.1	–
Lake Poygan				
Poygan Land Co. (1 and 2)	124.5	89.8	100.2**	63.2
Boom Bay	35.8	80.6	52.5	13.2
Willow-Pumpkinseed Cr.	0	0	19.2[a]	–
Total	160.3	170.4	171.9	–
Grand total	–	473.6	348.0	–

* In 1977, only the Allen's Marsh Study Area was photographed, and it had 24.0 acres of wildrice.

** Most of stand comprised of relatively low stem density.

[a] Minimum acreage; total acreage not determinable due to incomplete aerial photography coverage.

and wave action. Furthermore, physiological changes in floating leaves likely severely limits or curtails respiration and photosynthesis when rising water levels inundate these leaves (Aiken et al. 1988).

Site specific factors probably account for the variability in wildrice abundance and density among areas. These factors probably included sediment nutrient availability (Fannucchi 1983), water turbidity, exposure to wave action, carp feeding and spawning concentrations, motor boat activity (Dore 1969), and wildrice plantings by conservation clubs (A. Techlow, pers. comm.). However, water level fluctuations likely dictated abundance of wildrice on a system-wide basis.

Phenology. Wildrice seed germinated in late April through early May at various sites during 1976-82 (Fig. 10a). Water temperatures averaged for several locations and years were 10-15 C at this time (Fig. 10b). Wildrice plants grew rapidly during May and early June as water temperature increased from 15 C to 23 C (Fig. 10b, 10c). Foliage reached the water surface in mid-May to mid-June, and the floating leaf stage continued through mid-June to early August (Fig. 10a). Plant stems then erected from the water surface in mid-June to early August (Fig. 10a, 10d). Flowering began in July when water temperatures reached their summer maximums of 23-25 C, and most plants flowered by mid- to late-August (Fig. 10a, 10b, 10d). In most wildrice stands, seed development was evident by mid-August, and seeds were shed throughout September and early October (A. Linde, Wis. Dep. Nat. Resour., unpubl. data).

The occurrence of phenological events varied by 2-3 weeks during the study, depending on year, site, and water depth. Wildrice in the AMSA reached the water surface about 7-10 days later and plants remained in the floating-leaf stage about 3 weeks longer in 1980 than in 1977 (Fig. 10c, 10d).

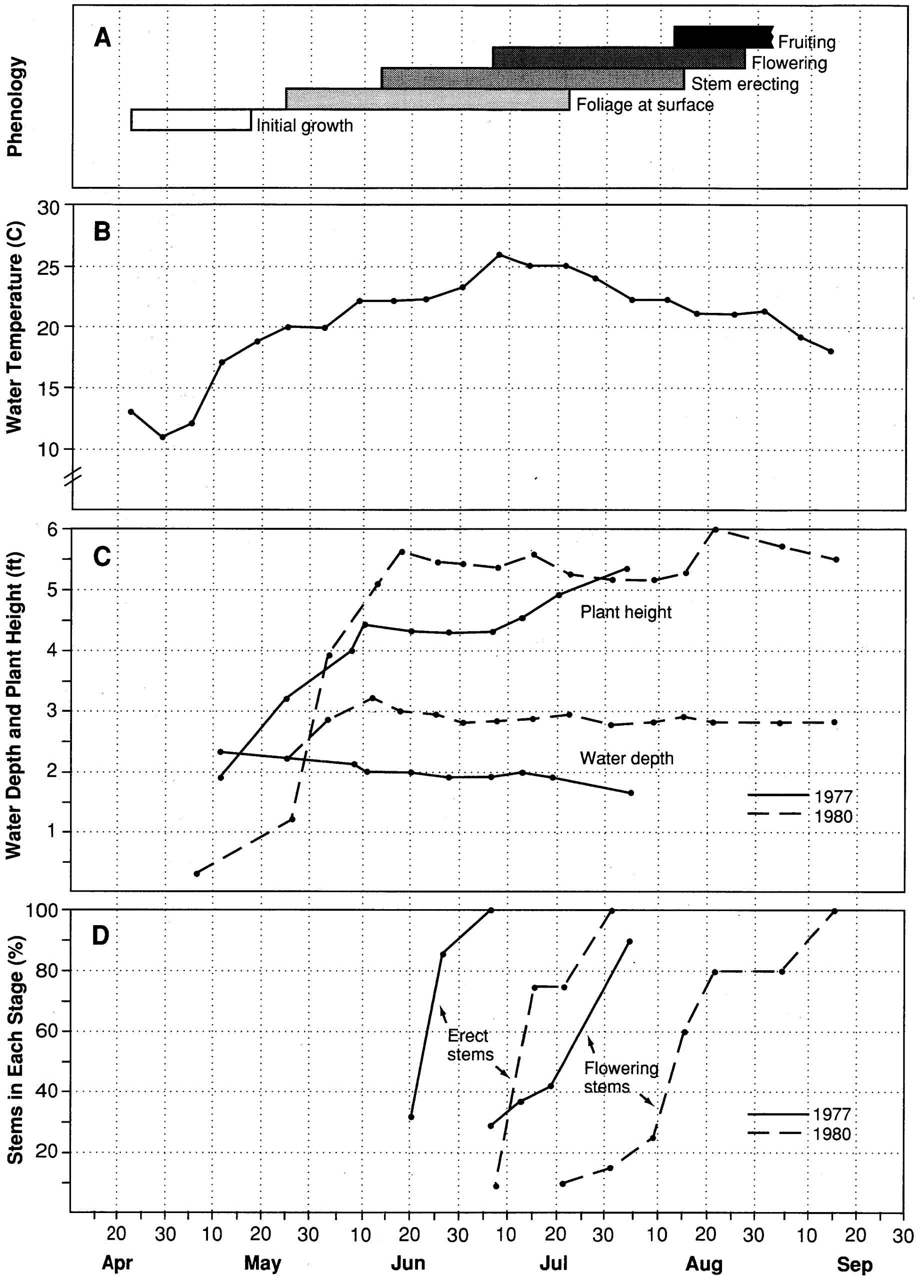


Figure 10. *Wildrice phenology for various locations during 1976-82 (a), water temperature averaged for several sites and years (b), and wildrice stem growth and phenology for systematically sampled stems from a "representative" stand at Allen's Marsh Study Area during 1977 (N = 20-31 stems) and 1980 (N = 11-21 stems) (c and d) in the Upper Winnebago Pool Lakes.*

This delayed emergent and flowering stages 2-3 weeks. Delayed phenology in 1980 possibly was due to colder water temperatures in spring (although no data were available for 1980) that delayed germination and to greater water depths at sampling sites (Fig. 10c). Deeper water prolonged the floating leaf stage, delaying flowering in a Lake Erie marsh (Thomas and Stewart 1969).

Sediments. At the AMSA and the Willow-Pumpkinseed creeks area (Fig. 3), sediments underlying wildrice stands were primarily silty and sandy with a mean organic content of 10% (Table 2). Wildrice displayed wide tolerance for various bottom sediments, except gravel, in the UWPL in 1969 (Harriman 1970).

In other North American locations, silty-organic sediments provided optimum habitat, but most substrates provided suitable habitat (Dore 1969, Kahl 1991). Sediment fertility and micro-nutrient availability can affect wildrice distribution and abundance (Fannucchi 1983, Aiken et al. 1988).

Water Depth. Wildrice tolerated maximum water depths of 5.9 ft and 4.4 ft in May-June, and 5.8 ft and 4.3 ft in July-August at the AMSA in Lake Butte des Morts in 1978 and at the Poygan Land Company area in Lake Poygan in 1981, respectively (Fig. 2). Depth tolerance of wildrice at the AMSA in 1978 likely reflected maximum depth for the entire period of 1975-79.

The wildrice stand at the AMSA expanded lakeward annually from 1975 to 1978 (Table 1). Size of this stand remained stable from 1978 to 1979, but density appeared to decrease in 1979. Low and declining water levels from July to September in each year of 1975-77 may have induced greater seed productivity, as found in Minnesota (Moyle 1944). In 1978, water levels remained relatively high from May-September, perhaps reducing seed production and subsequent plant density in 1979.

Extrapolation of water depths for wildrice stands from measurements taken in August 1969 (Harriman 1970) to other months that year yielded depth maxima of 3.9 ft in April, 4.5 ft in May-June, and 4.6 ft in July 1969 for the UWPL. Optimum water depths for several varieties of wildrice in other North American locations were 0.3-3.6 ft, and the range was 0.3-4.5 ft (Stoddard 1960, Dore 1969, Thomas and Stewart 1969, Kahl 1991).

Table 2. *Texture and organic content of sediments at wildrice, common reed, and round-stemmed bulrush stands in several locations of the Upper Winnebago Pool Lakes, 1975-79.*

	Texture				Organic Content	
Species	No. of Samples*	Sand (mean %)	Silt-sand (mean %)	Silt (mean %)	No. of Samples*	Mean %**
Wildrice	21	24	29	48	20	10 (16.8)
Common reed	2	50	0	50	8	15 (10.2)
Bulrush	12	33	67	0	19	10 (10.3)

* Number of 6-inch core samples for 2 stands of wildrice (Allen's Marsh Study Area, Lake Butte des Morts and Willow-Pumpkinseed Creeks Area, Lake Poygan) and bulrush (Allen's Marsh Study Area and Sunset Bay of Lake Butte des Morts), and 1 stand of common reed (northeast of Terrell's Island).

** Standard deviation in parentheses.

PHOTO: A. LINDE

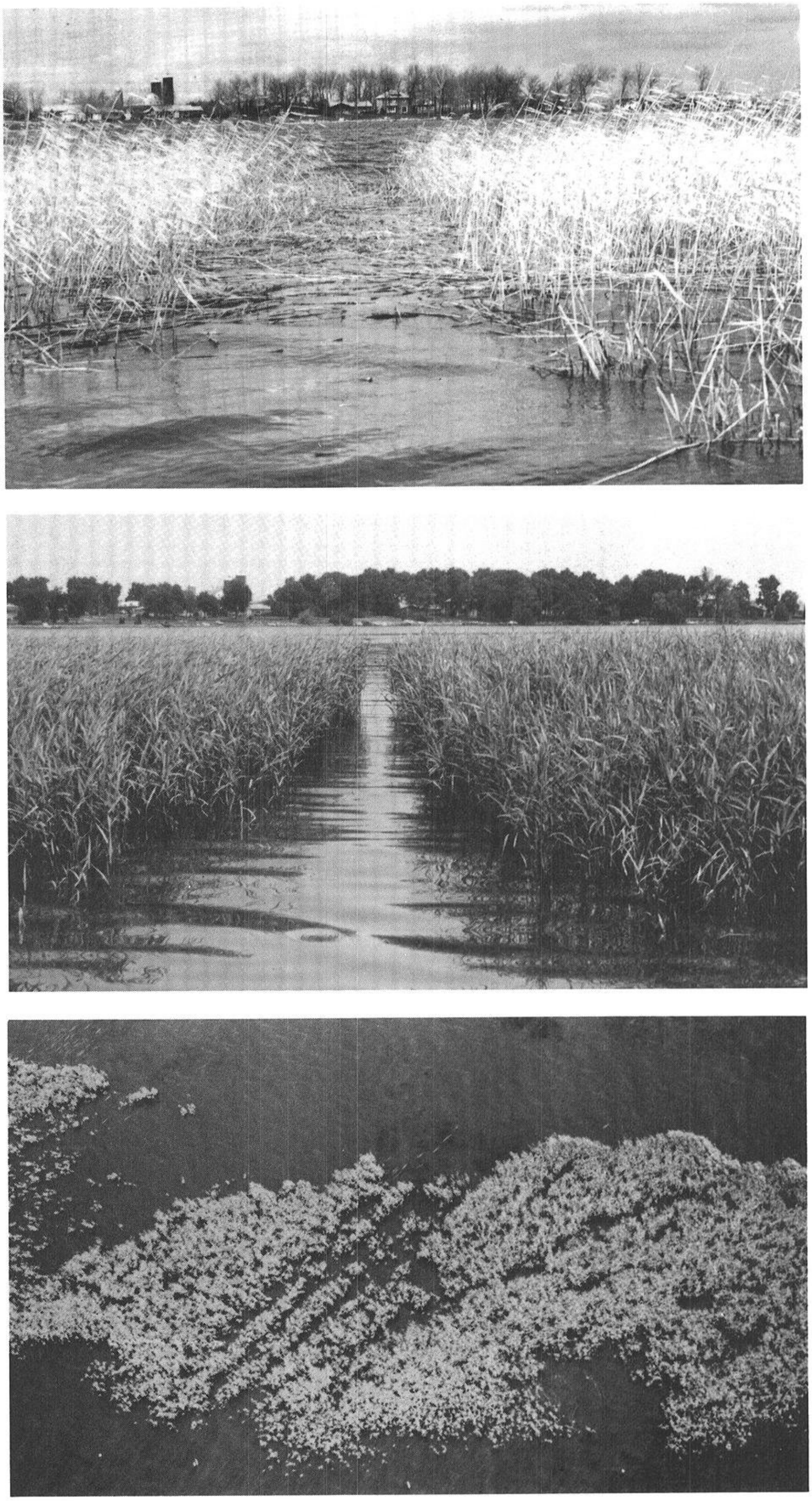
A dense stand of wildrice increased in size annually from 1975-78 in the Allen's Marsh Study Area, Lake Butte des Morts.

Common Reed

Distribution and Abundance. Common reed was abundant in adjacent marshes during the study but occurred only at widely distributed sites within the lakes. Typically, it occurred in small, dense monotypic stands. Most stands within the lakes represented remnant margins of marshes and shorelines from the mid-1800s (Figs. 5, 6). These remnant stands of common reed have remained quite stable since the late 1930s (Linde 1975). However, long-term high water levels producing water depths of 3.0-4.5 ft at the outer margins of most stands probably constituted the primary factor limiting expansion. These water depths stress plants and make them vulnerable to many other harmful agents.

Wave action, boating, snowmobiling, and carp may have interacted with high water levels to restrict expansion of these isolated stands into adjacent areas with comparable water depths, and may have prevented reestablishment of stands in other locations. Waves damaged new shoots from transplanted rhizomes of common reed directly and indirectly by depositing algae and other debris on these stems, subsequently submerging or severing them during this study.

Boats and snowmobiles apparently have damaged stems along the margins and within common reed stands. Numerous damaged stems along the margins of stands and paths through stands bordered by many damaged stems were associated with heavy fishing pressure along the edges and within stands during this study. Furthermore, several narrow paths through common reed stands during summer corresponded to location of snowmobile paths during winters of this study (A. Linde, unpubl. data), although snowmobiles may have used existing paths created by other activities, such as boating. Frequent boat passage through these paths may be maintaining and widening them.



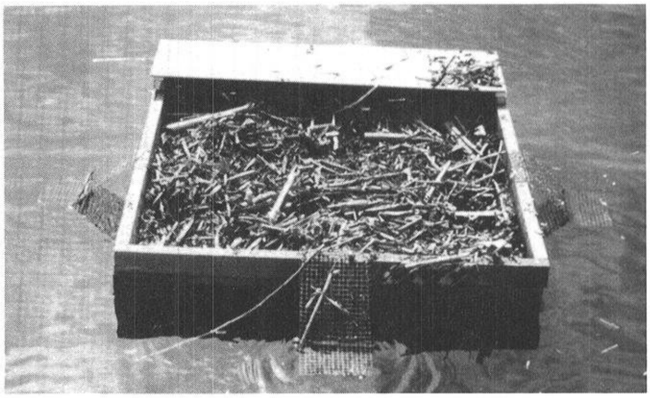
PHOTOS A LINDE

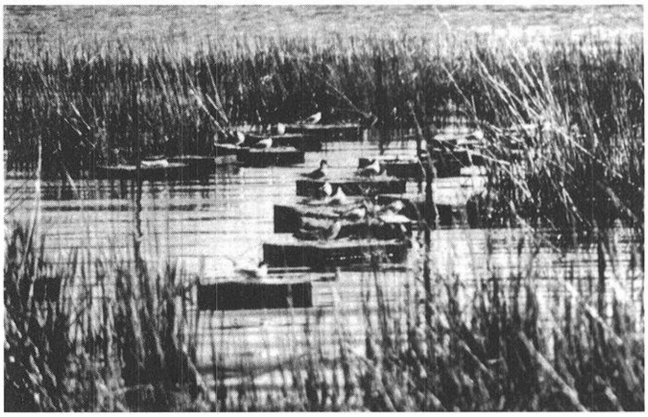
Broken, flattened residual stems of common reed in spring provide evidence of a snowmobile path from winter (top) that remains throughout summer in Sunset Bay, Lake Butte des Morts (middle), where numerous paths are evident through the same stands (bottom).

Several obvious boat channels were investigated during summer 1991, and numerous green stems were found cut or broken below the water surface (R. Kahl, pers. obs.). Anglers noticing these rudimentary paths likely followed them, damaging more stems and further widening paths. Lastly, extensive carp activity apparently damaged and severed many small shoots in several common reed stands along the northeastern shore of Lake Winneconne during May 1980 (A. Linde, unpubl. data).

These factors may have damaged established common reed stands by breaking off aerial stems that transport oxygen to rhizome systems. Cutting or breaking green stems in mid-summer probably causes greater damage by reducing photosynthetic tissue, thus reducing energy to rhizomes as well as reducing aeration. Cutting aerial stems of common reed below water reduced aeration to rhizomes and decreased bud and new shoot formation with the worst damage resulting in July and relatively little damage occurring in October-November in a European study (Haslam 1970). Reduced bud formation in mid- to late-summer can result in fewer viable stems produced the next year. Most damage likely occurs along outer margins of stands and this could limit bud formation and rhizome elongation at the terminal portion of existing rhizomes. Sediment fertility differences (Haslam 1970) at edges of exposed common reed stands could also limit their expansion. Lastly, ice shoves during spring breakup may damage rhizomes and shear off buds resulting in thinner stands that growing season.

Dense common reed stands within the lakes provide living breakwaters, cover, and nesting and egg-laying substrates for fish and wildlife, thereby constituting an extremely valuable resource in the UWPL. The endangered Forster's tern formerly relied on mats of residual stems in common reed stands in the UWPL for nesting material and for protected nesting sites. In recent years, artificial platforms have largely replaced natural substrate as safer, more reliable nest sites because rising water levels in spring and typically high late-spring and summer water levels break apart natural nesting mats and flood nests (A. Techlow, pers. comm.). However, artificial platforms are still placed in the protected interior of common reed stands. Common reeds also provide important fishing and hunting areas for sportspersons.





Forster's terns typically nested on mats of residual stems within common reed stands, but high water levels in May-June of most years destroys these mats and nests (top). Artificial nesting platforms have substituted for the natural substrate (middle photos), but success of these platforms still relies on placement within the protective interior of common reed stands (bottom).

PHOTOS: A. LINDE AND B. EICKHORST

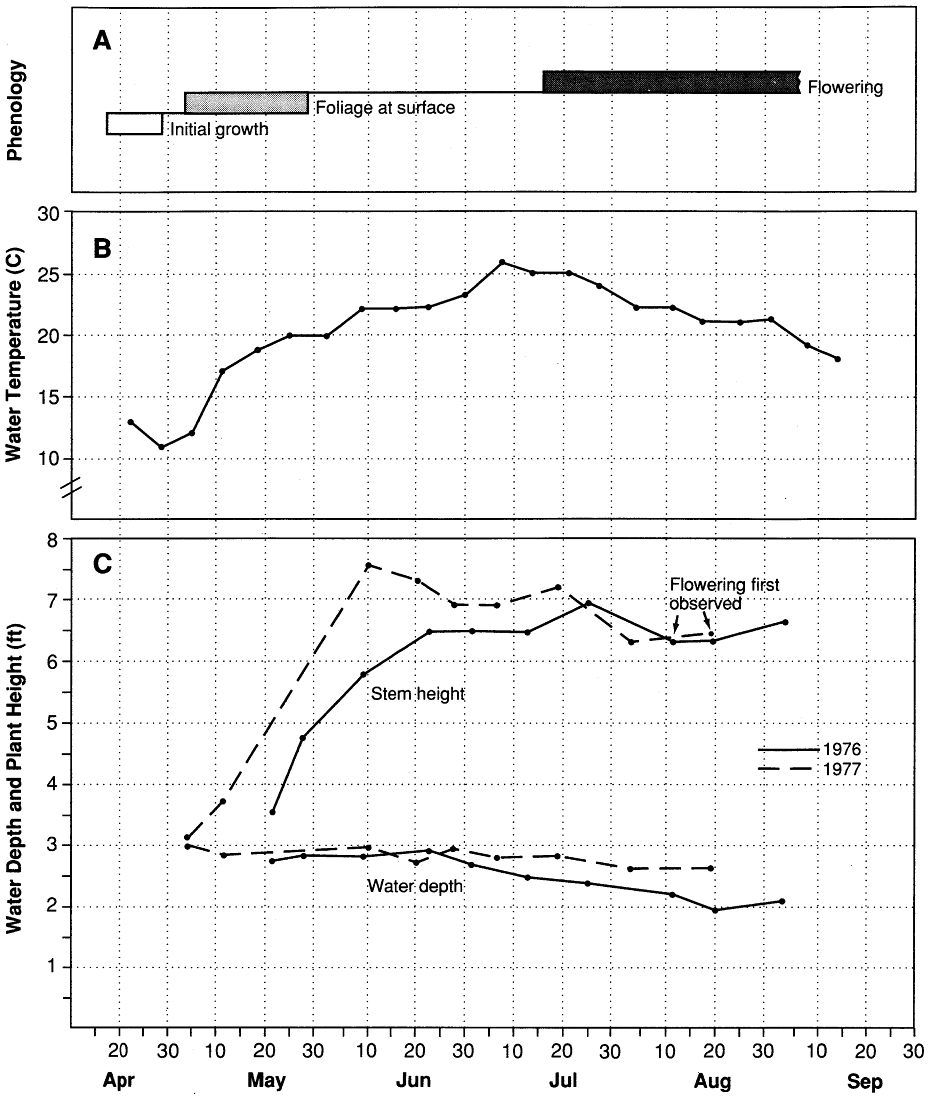


Figure 11. *Common reed phenology for various locations during 1976-82 (a), water temperature averaged for several sites and years (b), and common reed stem growth and phenology for systematically sampled stems from a "representative" stand in Sunset Bay, Lake Butte des Morts, during 1976 (N = 53-90 stems) and 1977 (N = 30-39 stems) (c) in the Upper Winnebago Pool Lakes.*

Phenology. Common reed is a perennial that produces new shoots in spring from rhizome buds formed primarily in late summer of the previous year. Growth of these shoots depends on energy stored in over-wintering rhizomes. Rhizomes in the UWPL initiated growth in mid- to late-April when water temperatures reached 10-15 C (Fig. 11a, 11b), although water temperature was not measured near any common reed stand. Stems emerged from the water throughout May, and grew rapidly during late May through mid-June (Fig. 11a, 11c). Maximum stem height was attained in mid- to late-June (Fig. 11c). Inconsistent stem heights from mid-June through August reflect the variable location of stems sampled within the stand and the inherent bias associated with subjective selection of stems for measurement. Plants in deep water typically produced taller stems than plants in shallow water. Average stem height was weakly correlated with water depth ($r^2 = 0.33$, $P = 0.08$) among 8 common reed stands in 1981. Seeds are rarely produced and require very shallow water (less than 0.5 inch) or moist mudflats to germinate (Haslam 1971*a*).

Common reed flowered from mid-July to mid-September in various locations and years (Fig. 11a). Panicles collected throughout September 1976 yielded few seeds, mostly in late September. Phenology varied considerably among sites and years. Plants in shallower water generally developed earlier, probably due to faster rising sediment temperature and a greater proportion of stem emerged than in deeper water. Unfavorable temperatures or water conditions delay emergence of buds (Haslam 1969*b*) and water depth and fluctuations, nutrient availability, grazing, salinity, and stability of the stand affect stand height (Haslam 1971*b*).

Sediments. Sediments at a common reed stand in the AMSA consisted of sand or silt with a mean organic content of 15% (Table 2). Sand and gyttja (dark, fine-grained organic sediments with high moisture content) supported common reed stands at several locations in the UWPL in 1969 (Harriman 1970). Sediments at common reed stands in the deepest waters were always sand. In several other localities, common reed occurred on most substrates but demonstrated a preference for sandy-organic sediments (Haslam 1972, Hutchinson 1975, Kahl 1991).

Water Depth. Common reed tolerated maximum water depths of 4.3 ft in April, 4.7 ft in May, 4.6 ft in June, and 4.1 ft in July and August at Sunset Bay, Lake Butte des Morts during 1976. Common reed in mid-lake stands typically grew in water depths of 3.0-4.5 ft. During August 1969, water depths at various common reed stands in the UWPL were 1.8-4.8 ft (Harriman 1970), which were extrapolated to maximum monthly means of 4.7 ft in April, 5.3 ft in May and June, and 5.4 ft in July 1969. At several other localities, optimum water depths were 0-3.3 ft, and the maximum water depth in the temperate zone was 6.6 ft (Haslam 1970, 1972).

Common Reed Re-establishment

Attempts to re-establish common reed resulted in varying degrees of success depending on size and development of harvested clumps, storage time and method, and transplanting method. The size of rhizome clumps and degree of damage to rhizomes and shoots during transplantation determined initial planting success.

Plantings stabilized and surrounded with sandbags in Lake Winneconne produced no new green shoots, although the sandbags effectively protected plantings. Rhizome clumps were harvested and transplanted on the same day (26 April 1977), but transplanting resulted in severance of all residual stems and new shoots. This severe damage probably contributed to complete failure of these plantings.

Only 2 of 16 plantings on 6 and 13 May 1977 stabilized with tires in Lake Winneconne survived into the fourth growing season (Table 3). Nine plantings failed during the first growing season, 3 died the second growing season, and 2 perished the third season. Early failure of transplants was related to size of the rhizome clump and especially to the number of intact stems at planting. Rhizomes and shoots sustained varying degrees of damage during harvest and planting, but at least 1 green stem remained intact for each of these plantings. All plantings failing the first season had 5 or less stems at planting. Only 1 planting with fewer than 5 stems survived into the second season.

The longest-surviving transplants stabilized with tires in Lake Winneconne (B and I) produced additional rhizomes and stems each year (Table 3). Phenology and maximum height of the most vigorous planting (B) were similar to stands at other locations, although height was approximately 1 ft less than maximum height in the control plot of a nearby established stand. In contrast, planting I produced stems with an average height of about 3 ft shorter than stems in the control plot. Furthermore, these stems attained maximum height in late August to early September, or approximately 2 months later than the control plot. Both of these plantings probably shunted energy into production and growth of new shoots and rhizomes, which reduced maximum stem height, especially of planting I during the first season.

Although plantings B and I (Table 3) appeared vigorous at the end of the third growing season, both failed in late spring and early summer of the fourth growing season 1980. Inadequate planting depth inside tires partially contributed to early demise of plantings. Plantings B and I produced horizontal rhizomes that were forced over the top of the tires and into the water column, reducing rhizome and root absorption of nutrients and minerals from sediments. This misdirection of rhizomes probably also wasted energy in growth of new rhizomes that produced fewer new stems.

Table 3. *Relative vigor of common reed rhizome transplants at the end of each growing season, Lake Winneconne, 1977-79.**

Planting Method, Date, and Site	Initial No. Stems Transplanted	1977		1978		1979	
		No. Stems	Height (ft)**	No. Stems	Height (ft)**	No. Stems	Height (ft)**
Tire Stabilization							
6 May 1977[a]							
B	10	46	7.7	61	7.0	148	7.0
C	9	16	5.4	0	–	0	–
D	8	9	3.6	4	3.4	0	–
13 May 1977[a]							
H	9	45	6.2	13	3.9	0	–
I	3	16	5.3	22	5.8	39	6.4
J	2	3	4.0	0	–	0	–
K	1	3	4.0	0	–	0	–
Wire Stabilization							
26 Jun 1978[a]							
1	50			108	8.8	115	7.4
2	–			10	3.6	0	–
3	–			20	7.0	0	–
4	–			16	7.3	0	–
5	–			4	7.4	9	3.9

* All of 5 plantings on 26 April 1977 (sandbag-stabilized) died during the first season, and all of 4 plantings on 16 May 1978 (tire-stabilized) washed out during the first season.

** Height of tallest stem.

[a] Two plantings on 6 May 1977, 7 plantings on 13 May 1977, and 6 plantings on 26 June 1978 died during the first season.

Of the 11 Winneconne plantings stabilized with wire, 2 survived through the second growing season, but only 1 of these appeared vigorous at that time (Table 3). Six plantings perished the year of planting, and 3 more died during the second growing season. Harvesting and transplanting in late June probably severely stressed these rhizome clumps. Stems in established stands at various locations attained maximum height by mid- to late-June (Fig. 11) and probably had depleted rhizome nutrient reserves.

Plantings made on 1-2 June 1978 stabilized with tires in western Lake Poygan were less successful than in Winneconne; none survived through the third growing season. Of the 46 plantings, 35 survived through the first season, but 17 of these had less than 5 viable green stems at the end of that season. Surviving plantings at this time supported a mean of 7.1 green stems (SD = 5.8). Mean height of the tallest stem in each planting was 5.7 feet (SD = 1.5). By the end of the second season (1979) only 17 plantings remained alive with 7.8 green stems/planting (SD = 6.4) and a mean maximum height of only 3.7 ft (SD = 0.9). Green stems in all plantings except 1 were less than 5 ft tall in 1979, indicating that these plants were severely stressed. In late spring of the third season (1980), all surviving plantings produced only 3 small, green stems, and algae accumulations bent and severed these stems in early June. Greater water depth at the Poygan site likely stressed transplants more than at the Winneconne site (2.0-3.0 ft vs. 1.0-2.0 ft, respectively).

Accumulation of filamentous algae and plant debris on emerging green shoots in June of all years possibly contributed to decline of the plantings. Weight of this algae and debris, coupled with wave action, bent, severed or submerged shoots. This problem was acute in June 1980 when the last surviving shoots disappeared. Long-term stress and inadequate production of new shoots and horizontal rhizomes probably drained energy stores from planted rhizomes over several years, contributing to weaker stems and eventual transplant failure. Horizontal rhizomes, such as those planted, typically live for only 3-6 years (Haslam 1969*a*), and rhizomes survived a maximum of 3-4 years in this study. Furthermore, low water levels in winter could have exposed frail, overwintering rhizomes to damage from freezing (Haslam 1969*b*). Lack of residual stems necessary for gas exchange possibly caused further physiological stress to overwintering rhizomes.

Transplanting rhizomes after substantial growth of new shoots probably severely stresses plantings, especially if shoots have reached near maximum height and are damaged during transplanting as in the June plantings of this study. Rhizome carbohydrate reserves typically are depleted to near seasonal lows when stems reach maximum height (Fiala 1976). Afterwards, established plants probably initiate storage of nutrients and carbohydrates in rhizomes and formation of new buds for growth of stems in the following year, as documented for cattails in Wisconsin (Linde et al. 1976). In spring, buds emerge rapidly over several weeks to several months. Few new buds emerge and produce stems outside this period, and cutting of stems outside the emergence period severely injures the plant by eliminating most or all photosynthetic tissue (Haslam 1969*b*). Transplants in this study either seriously depleted rhizome reserves for production of new shoots after loss of original shoots, which delayed and reduced nutrient storage, or had completed the bud emergence stage and produced no new stems. Both alternatives would leave rhizomes with relatively low nutrient stores at the end of the growing season. Furthermore, low nutrient reserves probably preempted rhizome growth that typically occurs in late summer (Fiala 1976). Cattail rhizomes produced in previous years comprise the principal storage organ (Linde et al. 1976), and stress from injury that limits growth of new rhizomes over one to several seasons could affect long-term survival.

Round-stemmed Bulrushes

Distribution and Abundance. The UWPL supported small, widely distributed stands of round-stemmed bulrushes during 1975-82. Abundance of these species apparently declined from the 1930s to the 1960s (A. Techlow, pers. comm.). However, round-stemmed bulrushes were some of the most abundant emergents remaining in the UWPL during 1968-69, growing mainly in areas exposed to severe wave action (Harriman 1970). The factors restricting abundance and distribution of common reed probably also had the same impact on bulrushes. These include long-term high water levels, boats, snowmobiles, carp, and deposition of algae and detritus by waves.

Phenology. Round-stemmed bulrushes are perennials that regrow from overwintering rhizomes. In the UWPL, rhizomes produced new shoots in mid- to late-April when water temperatures reached 10-13 C at the sediment surface (Fig. 12a, 12b). Stems grew rapidly during late April through early June, emerged from the water in early to mid-May as water temperature quickly increased to 20 C, and attained maximum height in early to mid-June (Fig. 12a, 12b, 12c). Subjective selection of stems and variable sampling locations probably accounted for most of the variability in stem height after mid-June.

Water depth dictated maximum stem height and height above water of the emerged stem among 8 different stands ($r^2 = 0.98$, $P < 0.001$; $r^2 = 0.60$, $P = 0.01$, respectively) in 1981. Other site characteristics such as sediment type or site exposure had little affect on stem height. Round-stemmed bulrush plants in deep water compensated photosynthetically by producing taller stems at the rate of about 1.2 ft additional stem length for each 1.0 ft increase in water depth ($y = 2.86 + 1.19\ x$). Although total stem length increased at a greater rate than water depth, the emerged proportion of total stem length actually declined with increasing water depth ($r^2 = 0.98$, $P < 0.001$). Round-stemmed bulrushes produced 69% of the stem above the water surface in the shallowest areas (1 ft water depth) and exhibited an 8% reduction in the proportion of stem emerged for each 1.0 ft increase in water depth ($y = 0.77 - 0.08x$). The minimum proportion of stem emerged—or compensation point—was 43-44% at maximum water depths of 4.3-4.5 ft during June to August. Round-stemmed bulrush plants probably augmented the amount of photosynthetic stem tissue above the surface to compensate for greater energy demand in producing and maintaining a taller stem at greater water depths and to enhance nutrient storage in rhizomes through this longer pathway.

Floral development commenced in late May to early June, and continued through early September (Fig. 12a, 12d). Peak flowering over the entire lake system occurred from mid-June to mid-August when water temperature was >20 C (Fig. 10b, 10d). Timing and intensity of flowering varied among sites each year, but when averaged for all sites, flowering remained fairly constant among years from 1979-81 (Fig. 12d).

Rhizomes of round-stemmed bulrushes stored nonstructural carbohydrates over winter. Plants mobilized and quickly depleted these energy stores in spring for rapid growth of stems to maximum height by early to mid-June (Fig. 12c, 12e). Total nonstructural carbohydrates (TNC) reached a seasonal low in early to mid-June at the onset of flowering. However, plants had attained maximum height and probably maximum photosynthetic tissue, so they could shunt sufficient energy into flowering and rhizomes. Rhizomes then accrued TNC from mid-June to a peak in September at the onset of senescence. Cattail, common reed (Fiala 1976), and a bulrush, *Schoenoplectus lacustris* (Steinmann and Brandle 1984), displayed similar patterns of carbohydrate storage and metabolism in rhizomes that

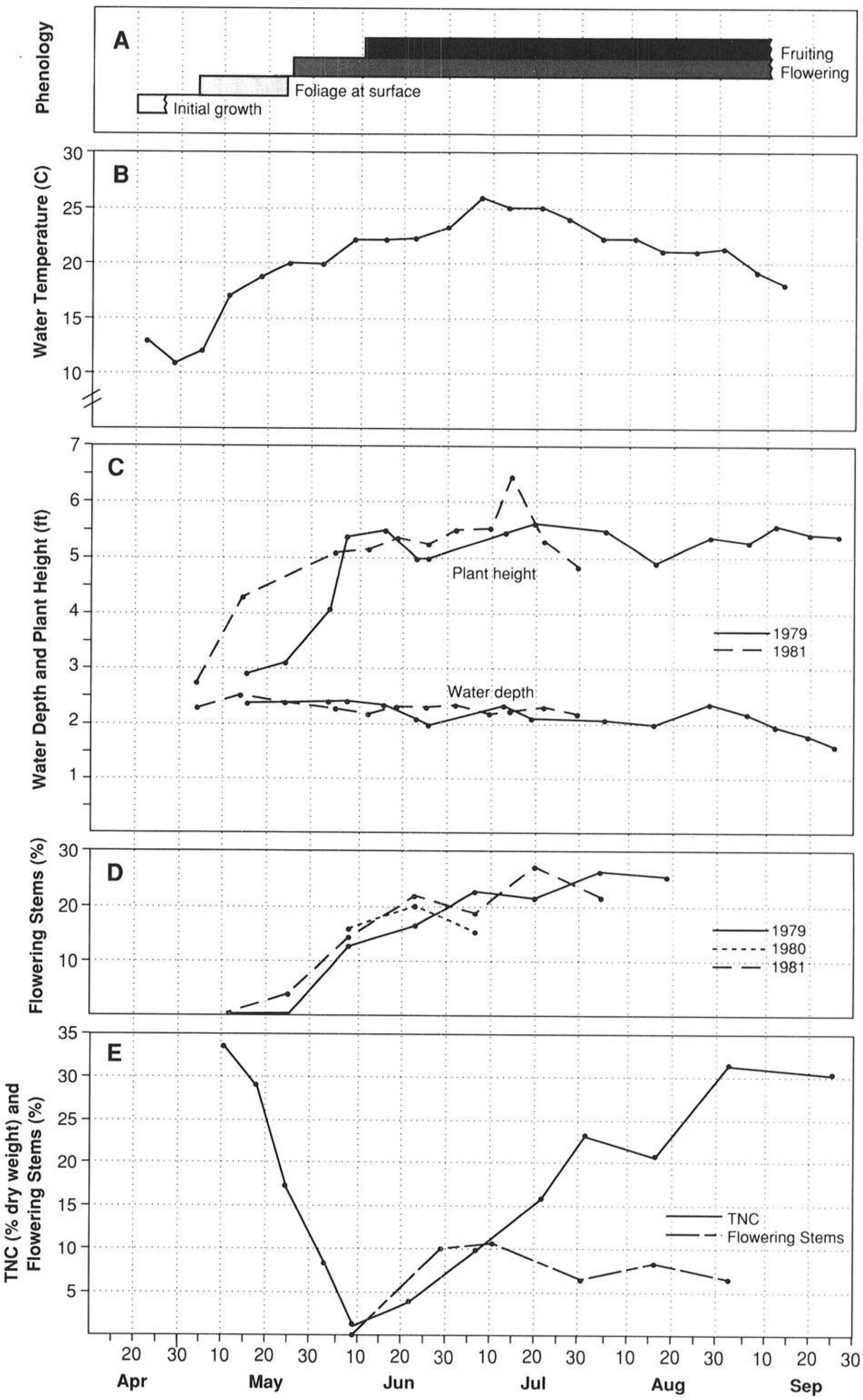


Figure 12. *Round-stemmed bulrush phenology for various locations during 1976-82 (a), water temperature averaged for several sites and years (b), round-stemmed bulrush stem growth for systematically sampled stems from a "representative" stand at Allen's Marsh Study Area during 1979 and 1981 (N = 20-30 stems except on 22 June 1979 and 4 May 1981 when N = 12 and 5, respectively) (c), flowering phenology of systematically sampled stems for irregular sampling dates averaged by 2-week intervals for 3 locations during 1979-81 (d), and total nonstructured carbohydrate (TNC) content of rhizomes during late spring and summer 1978 at Allen's Marsh Study Area, Lake Butte des Morts (e) in the Upper Winnebago Pool Lakes.*

were associated with rapid growth in spring. Severe damage to photosynthesizing stems during the period of minimum rhizome TNC could prove fatal to plants, as suggested for cattail (Linde et al. 1976).

Moderate to severe damage to stems over several years in June and early July could reduce long-term survival, and thus reduce stand size and density, by reducing energy assimilation and slowly decreasing energy reserves in rhizomes. Other limiting factors, such as high water levels, would further stress plants and diminish survival. During favorable conditions, especially years of low spring-summer water levels, re-colonization would proceed slowly because the plant relies on rhizome migration at these inundated sites.

Although seed production is common and often prolific, seeds require very shallow water or exposed mudflats for germination and survival of seedlings (van der Valk and Davis 1978). Consistently high water levels in the UWPL during the growing season prevented most reproduction from seeds at shoreline and in-lake sites.

Sediments. Round-stemmed bulrushes in 2 representative stands in the AMSA and Sunset Bay of Lake Butte des Morts grew in sand or silty sand sediments with a mean organic component of 10% (Table 2). Hard-stemmed bulrush stands surveyed in the UWPL during 1968-69 inhabited areas only with sand or gyttja sediments (Harriman 1970). Hard, compacted sediments, especially sand, contributed to optimum habitat for hard-stemmed bulrush in several other water bodies (Martin and Uhler 1939, Kahl 1991).

Water Depth. Round-stemmed bulrushes in 8 stands tolerated a wide range of water depths ranging from 1.5-4.5 ft in April-June and 1.7-4.4 ft in July-August 1981. During August 1969, hardstem bulrush occurred in water depths of 1.0-4.1 ft in the UWPL (Harriman 1970). Maximum depth of colonization extrapolated from August 1969 reached 4.0 ft in April, 4.6 ft in May-June, and 4.7 ft in July 1969. At other locations, optimum water depths for hardstem bulrush were 1.0-3.0 ft, and maximum water depth was 5.0 ft (Moyle and Hotchkiss 1945, Dabbs 1971).

Spike Rush

During 1975-82, spike rush was sparsely distributed in small stands at 6 locations in the UWPL. Information on abundance prior to 1975 is lacking.

Spike rush initiated growth in mid- to late-April, and stems reached the water surface in early to late May. Stems attained maximum height in late May through mid-June. Plants then flowered until mid- to late-July.

Water depth determined maximum stem height among stands ($r^2 = 0.96$, $P < 0.001$). However, stem length increased at a rate only slightly greater than water depth ($y = 1.43 + 1.04\ x$). Proportion of emerged stem was negatively related to water depth ($r^2 = 0.83$, $P < 0.001$) and decreased at the rate of 7% for each 1 ft increase in water depth ($y = 0.56 - 0.07\ x$). The apparent compensation point for emerged proportion of stem approximated 28-29% at maximum depths of 3.8-4.0 ft in June-August. Spike rush produced a basal stem 1.43 ft tall in the shallowest zones compared to 2.86 ft for round-stemmed bulrushes at similar depths. At water depths of 3.8-4.0 ft, round-stemmed bulrushes had a compensation point of 45% vs. 29% for spike rush. Such differences suggest that spike rush photosynthesizes and assimilates energy and nutrients more efficiently, produces more stems per length of rhizome, or relies on a less elaborate rhizome system than round-stemmed bulrushes. Spike rush tolerated a maximum water depth of 3.5-3.6 ft in April and 3.8-4.0 ft in May-August for 9 stands in 1981.

Spike rush demonstrated growth form, phenology, and habitat requirements similar to round-stemmed bulrushes. These species often grew in close association, suggesting that the same factors limit both species. Spike rush can survive at wind-swept, exposed locations and comprises a valuable component of the macrophyte community in the UWPL.

Stiff Arrowhead

This species occurred in small, scattered patches throughout the UWPL during 1975-82. Stiff arrowhead was abundant and widely distributed during the 1930-60 period, apparently having colonized many of the locations formerly supporting floating bog and shallow-water marsh (A. Techlow, pers. comm.). Stiff arrowhead remained abundant in the lakes during 1968-69 (Harriman 1970). This species preferred somewhat exposed sites with relatively deep water (Harriman 1970).

This perennial species typically overwinters as a starchy tuber. Phenology of stiff arrowhead was documented only after leaves reached the water surface in late May to mid-June. Plants quickly attained maximum height and initiated flowering in late June to mid-July. Flowering continued through mid- to late-August.

Water depth determined stem height ($r^2 = 0.93$, $P < 0.001$) for 7 stands, and stem height increased at approximately the same rate as water depth ($y = 1.38 + 1.0\ x$) in 1981. Stiff arrowhead expended only enough additional energy in stem elongation to keep the slightly expanded leaf blade emerged. At maximum water depths of 3.9-4.0 ft during June-August, stiff arrowhead maintained a minimum proportion of 22-23% of the stem and leaf blade above the surface. This represented the apparent compensation point of photosynthetic tissue required to support the plant and produce overwintering propagules.

The lower compensation point for this species vs. round-stemmed bulrushes probably reflected reliance by stiff arrowhead on expanded leaf blades as the primary photosynthetic tissue and possibly the less demanding overwintering strategy of relying on discrete tubers rather than on elaborate rhizome systems.

Stiff arrowhead colonized a maximum depth of 3.5 ft in April and 3.9-4.0 ft in May-August during 1981. It tolerated water depths of 1.5-4.0 ft in the UWPL during August 1969 (Harriman 1970), which extrapolated to 0.9-3.4 ft in April, and 1.5-4.1 ft in May-July.

During 1968-69, stiff arrowhead exhibited wide tolerance of all sediment types except gravel (Harriman 1970). Stiff arrowhead in Pool 9 of the Upper Mississippi River produced greater biomass on coarser sediments, and sedimentation introducing fine clay and silt particles into backwaters reduced biomass (Clark and Clay 1985).

Factors that limited abundance likely include water turbidity, prolonged high water levels, eutrophication, carp, and deposition of algae and detritus by waves. The floating-leaf stage in late May to early June presumably represented a critical period when the plant was vulnerable to damage from rapidly rising water levels, waves, and algae accumulations. Well-developed root systems from buried tubers probably limited uprooting from firm sediments. However, carp apparently uprooted many mature plants from areas with soft sediments during summer 1991 (R. Kahl, pers. obs.), and strong waves presumably could cause similar uprooting in these areas. Increasing water levels during and after the floating-leaf stage could submerge the leaf blade and reduce photosynthetic efficiency. Several consecutive years of abnormally high water could decimate stands near the maximum depth limits. Lower water levels would encourage expansion of existing stands and establishment of new stands. Low water levels (2.5-2.7 ft at the Oshkosh gage) in spring and early summer 1987 apparently allowed several stiff arrowhead stands in Lake Poygan to expand (R. Kahl, pers. obs.).

Submerged Macrophytes

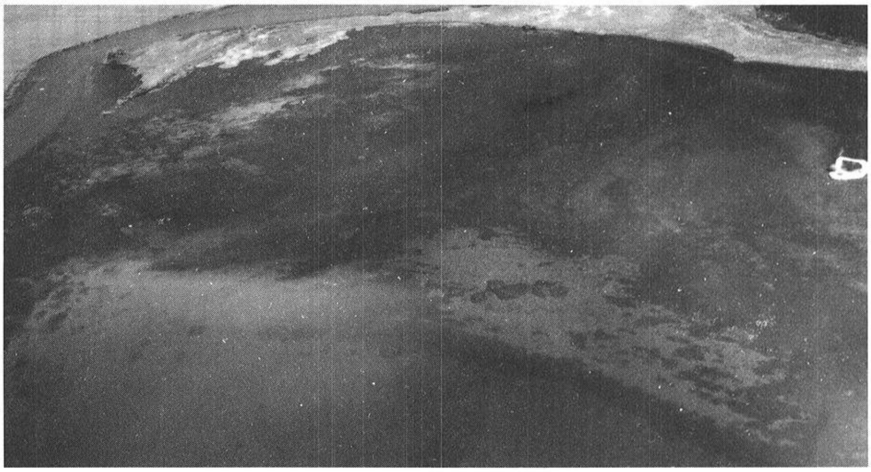
Distribution and Abundance. During 1975-79, Lakes Butte des Morts and Poygan supported about 1,650 acres of submerged macrophytes in 8 locations (Table 4, Fig. 3). Lake Winneconne probably supported another 150-200 acres, primarily south and east of Clark's Point. Submerged macrophytes existed elsewhere in scattered, small beds. The abundance of submerged macrophytes remained relatively stable in most locations from 1975-79. Varying turbidity on flight dates probably accounted in part for apparent differences in plant abundance among years by concealing submerged macrophytes at outer margins of beds documented with aerial photography.

Species composition along submerged macrophyte transects apparently differed among 8 sites and between May-June and July-August sampling periods. However, the rake technique and sampling design precluded statistical analysis of species composition and abundance differences among sampling periods, years, and sites. The most abundant species system-wide during May-June were coontail, water milfoil, wildcelery, sago pondweed, and Canadian waterweed (Table 5). In contrast, wildcelery attained dominance at 4 of 8 locations and co-dominance at 1 other location during July-August. Other important species in July-August included sago pondweed, water stargrass, water milfoil, and Canadian waterweed.

Uprooted stiff arrowhead stems are often noticed in areas with soft sediments and heavy carp spawning activity.

Table 4. *Acreage of submerged macrophytes for 8 locations in Lakes Butte des Morts and Poygan determined from aerial photography in July to early September, 1975-76 and 1978-79.*

	Acreage by Year			
Location	**1975**	**1976**	**1978**	**1979**
Lake Butte des Morts				
Sunset Bay	–	62.4	50.0	49.0
Scott's Bay	–	294.7	246.8	218.7
Nickel's Marsh-west	–	129.6	150.7	–
Nickel's Marsh	–	79.4	71.7	77.6
Terrell's Island	–	–	128.6	–
Total	–	–	647.8	–
Lake Poygan				
Poygan Land Co. (1 and 2)	363.8	391.0	416.6	396.2
Boom Bay	191.4	253.3	249.9	262.7
West shore	347.3	354.8	–	–
Total	902.5	999.1	–	–



Submerged macrophyte abundance was documented with aerial photography, but water turbidity often concealed outer margins of beds, as in the lower left of this photo.

Table 5. *Species mean percent of total submerged macrophytes collected along rake sampling transects in 8 locations of Lakes Poygan and Butte des Morts, 1977 and 1979-82.**

	Wild Celery	Sago Pondweed	Canadian Waterweed	Coontail	Narrow-leaved Pondweeds**	Water Stargrass	Water Milfoil	Filamentous Algae	Clasping-leaf Pondweed[a]
Phenology Transects									
May-June	25.7	5.7	10.7	13.2	11.3	3.5	15.3	1.9	4.3
Lake Poygan	51.2	0.8	2.7	17.8	4.7	1.9	0.1	7.6	11.9
West shore	38.8	7.5	3.2	20.7	2.3	10.5	8.9	0	3.9
Poygan Land Co. (1)	tr	3.6	34.8	7.1	0.7	1.2	49.6	0	0.2
Poygan Land Co. (2)	12.9	11.0	12.2	17.0	37.6	0.3	2.4	tr	1.0
Boom Bay	3.3	21.8	6.8	20.4	10.0	3.6	18.1	1.7	1.4
Lake Butte des Morts	0.6	38.8	0.3	26.2	3.1	1.8	12.5	1.1	2.5
Springbrook	–	–	–	–	–	–	–	–	–
Scott's Bay	6.4	21.6	9.8	6.1	1.7	5.7	30.7	3.0	1.6
Allen's Marsh	2.9	5.1	10.2	28.9	25.1	3.4	11.2	1.1	tr
Sunset Bay									
Average	15.6	14.5	10.0	19.1	9.5	3.4	15.9	2.6	3.1
July-August									
Lake Poygan	63.4	3.4	12.7	1.4	3.5	7.3	5.4	1.3	1.0
West shore	86.8	tr	0.8	3.4	0.2	0.7	tr	4.8	4.1
Poygan Land Co. (1)	84.8	1.3	0.7	0.7	1.5	9.2	1.2	0	0
Poygan Land Co. (2)	4.9	tr	48.4	0	4.8	19.1	20.3	0	0
Boom Bay	76.9	12.1	0.8	1.5	7.4	0.1	0.1	0.5	0
Lake Butte des Morts	37.5	19.1	3.0	7.3	7.5	2.5	11.1	0.6	0.1
Springbrook	19.3	37.8	4.9	13.7	3.3	9.4	0.8	1.0	0.1
Scott's Bay	88.7	0.3	0.4	1.9	0.7	0.1	4.0	0	0
Allen's Marsh	14.0	31.0	2.0	2.1	1.3	0.5	38.9	1.2	0
Sunset Bay	28.1	7.3	4.7	11.4	24.8	0	0.8	0	0.1
Average	50.2	11.0	7.0	3.9	4.9	8.9	7.4	0.9	0.5
Relative Abundance Transects									
Lake Poygan									
West shore	85.3	4.5	0.6	3.4	0.8	0.8	tr	2.3	0.1
Lake Butte des Morts									
Sunset Bay	11.0	18.4	10.1	12.4	13.9	9.5	13.9	0	0

* Mean percent of wet volume or mean percent rake coverage of total submerged macrophytes, weighted by date and year of sampling (3-16 dates over 1-5 years for May-June and 4-12 dates over 1-4 years for July-August).

** Narrow-leaved *Potamogeton* spp.

[a] Primarily *Potamogeton richardsonii*, but also *P. crispus.*

Lake Poygan supported the largest submerged macrophyte beds (Table 4), which consisted primarily of wildcelery during July-August in all locations except the interior marshes of the Poygan Land Company (site 2; Table 5, Fig. 3). More heterogeneous beds existed in most sheltered bays of Lake Butte des Morts, except Scott's Bay where wildcelery dominated.

During August 1968-69 wildcelery occurred most frequently, closely followed by sago pondweed and American pondweed in the UWPL (Harriman 1970). Lake Poygan consisted of large expanses of open water supporting few aquatic beds in 1968-69. Habitat conditions possibly improved from 1968-69 to 1975-82; the UWPL apparently supported more submerged macrophytes during the latter period, especially wildcelery in Lake Poygan.

Site-specific factors such as water clarity, carp spawning and feeding concentrations, or exposure to severe wave action, especially in conjunction with sediment type, probably determined distribution and abundance of submerged macrophytes locally in the UWPL. System-wide, water clarity probably controlled abundance of submerged macrophytes.

Phenology. Differences in relative abundance of submerged species between May-June and July-August reflected differing phenology and species interaction (Fig. 13a). Water temperatures of 10-13 C apparently triggered growth of new foliage in mid- to late-April for the earliest species (Fig. 13a, 13b). This group consisted primarily of species that often overwinter in a vegetative state, such as coontail, water milfoil, narrow-leaved pondweeds, and Canadian waterweed (Fig. 13a). In contrast, the latest species, wildcelery and clasping-leaf pondweed, delayed growth until early to mid-May when water temperature was rapidly increasing from about 13 C to 17 C. Although sago pondweed began growing 2 weeks later than the earliest species, it flowered in early June about 1-2 weeks earlier than these species (Fig. 13a).

Water temperature had reached 20 C by this time. Wildcelery and water stargrass delayed flowering until mid- to late-July when water temperature reached the summer maximum.

In other studies, temperature stimulated growth at 10-12 C and 10-14 C for sago pondweed (Stevenson and Confer 1978) and wildcelery (Zamuda 1976, cited in Korschgen and Green 1989), respectively. Wildcelery in navigation pools of the Upper Mississippi River initiated growth in late May to early June, achieved maximum biomass production rates in mid- to late-July during flowering and rosette formation, and attained maximum biomass during fruit development in early August to early September (Sefton 1976, Donnermeyer 1982). Optimum temperatures for growth of wildcelery were 20-36 C in other studies (Korschgen and Green 1989). Water temperature exceeded 20 C by early June in this study, or about one month before foliage appeared at the surface and plants initiated flowering (Fig. 13a, 13b).

Sediments. Sediments along the 2 relative abundance transects with the most vegetation (transects B and C), dominated by wildcelery and sago pondweed (Fig. 2), consisted primarily of silty-organic and sand or silty-sand textures with mean organic content of 13-19% dry weight. Sediments with similar textures and organic content occurred along similarly shallow portions of the other transects that supported few or no submerged macrophytes. For data from all transects and species pooled, there was no apparent relationship between presence and abundance of submerged macrophytes vs. sediment texture and organic content. Presence of submerged macrophytes was independent of sediment texture (*P* = 0.38) for sandy vs. silty-organic sediments. Abundance (% coverage of a rake) also did not differ (*t* = 0.58, *P* = 0.56) between plots with sandy (6.8%

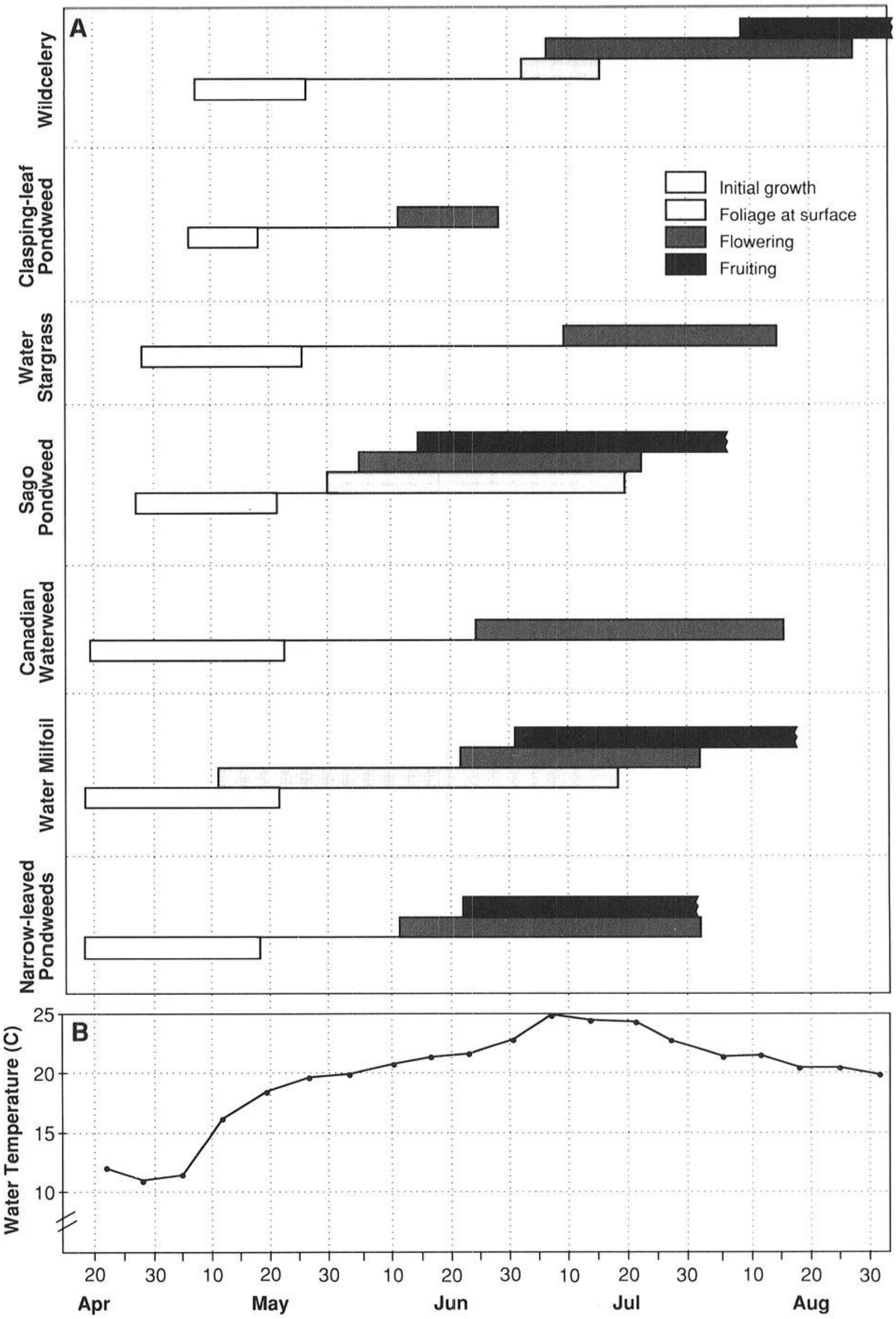


Figure 13. *Phenology of submerged macrophytes (a) and water temperature (b) averaged for various locations in the Upper Winnebago Pool Lakes, 1976-82.*

coverage) vs. silty-organic (8.1%) sediments. Lastly, sediment organic content did not differ for plots supporting vegetation (18.9% organic content) vs. plots without vegetation (18.3%) ($t = -0.18$, $P = 0.86$). During 1968-69, the most important species—wildcelery, sago pondweed, and American pondweed—exhibited wide tolerances of sediment from gyttja to peat and sand, yet large areas apparently with similar sediments and water depths remained unoccupied (Harriman 1970), as during 1975-82.

Both wildcelery and sago pondweed have demonstrated an adaptability to colonize many different substrates with widely varying texture and organic content in other locations (Korschgen and Green 1988, Kantrud 1990). Other factors such as wave action and turbidity probably exert a greater influence on distribution and abundance of sago (Kantrud 1990), and probably also wildcelery. Evidence from other studies suggests that sediment composition and nutrient and mineral availability usually determine abundance and distribution of submerged macrophytes within the photic zone (Barko et al. 1982). Increasing sediment organic matter may reduce sediment density and availability of nutrients (Barko and Smart 1986). In conjunction with light, nutrient availability in sediments may determine maximum depth of the macrophyte photic zone by limiting growth and preventing photosynthetic tissue from reaching and remaining within the photic zone. Exposure to varying wave energies further complicates ecological relationships through the influence of waves on sediment texture (Keddy 1985) and fertility, turbidity (Kadlec 1962, Wilson and Keddy 1985), and physical damage to plants (Jupp and Spence 1977).

Water Depth. Submerged macrophytes at various sampling locations inhabited maximum depths of 47-53 inches in Lake Butte des Morts, 51-55 inches in Lake Winneconne, and 55-61 inches in Lake Poygan during July-August of 1975-80. Wildcelery and sago pondweed typically occurred at greater depths than other species along transects during this time. Maximum depth of colonization varied between lakes and among areas within lakes as evidenced along the 5 relative abundance transects (transect A: 37-39 inches, B: 48-53 inches, and E: 29 inches for Lake Butte des Morts; D: 36-42 inches for Lake Winneconne; and C: 60-67 inches for Lake Poygan). Differing water clarity, species composition, wave exposure, and sediment nutrient availability probably accounted for these differences. Of most importance, site-specific factors likely altered water clarity locally. These factors included carp spawning and feeding, erosion of unstable marsh edge and shorelines, resuspension of soft organic sediments by waves and carp, and turbid inflow from tributary streams. Maximum depth of colonization by submerged macrophytes is determined primarily by water clarity (Spence 1982, Chambers and Kalff 1985).

During August 1969, turbidity limited submerged macrophytes to water depths less than 4 ft in the UWPL (Harriman 1970). The greater water depths tolerated by submerged macrophytes, especially in Lake Poygan, during summers of 1975-80, support the suggestion that macrophyte beds expanded from 1969 to the 1975-80 period. Significantly higher water levels occurred in June-July 1969 than for any year during 1975-80 (TSRT, $P < 0.05$). Abnormally high water throughout May-July 1969 conceivably eliminated submerged macrophytes at maximum depth limits by August. Greater flooding in 1973 (Fig. 7) should have reduced abundance of submerged macrophytes even more than in 1969. If so, submerged macrophytes quickly re-colonized outer margins of major beds by 1975-80.

Sago pondweed and wildcelery were encountered at depths exceeding 20 ft, but these species were found most commonly at depths of 1.5-16 ft elsewhere (Davis and Brinson 1980, Korschgen and Green 1989). These 2 species appear to be among the most turbidity-tolerant species of submerged macrophytes (Robel 1961, Davis and Brinson 1980). Sago pondweed produced dense foliage at the water surface by late spring to early summer before algal blooms drastically reduced water clarity in hyper-eutrophic Lake Koshkonong, Wisconsin (R. Kahl, unpubl. data). This growth strategy partly explains the apparent tolerance of turbidity.

Factors Affecting Macrophyte Abundance

Water Levels

The annual cycle of water levels for most years during 1975-84 generally followed the water regime adhered to since the late 1930s. Water levels peaked in May and June, then slowly declined throughout summer and early fall until November or December. A rapid drawdown from December through February or March provided for flood storage. However, differing precipitation patterns and slow response time to major precipitation and runoff events resulted in different mean monthly water levels among years and among months ($P < 0.001$ for both) (Table 6). Largest monthly differences among years occurred in October, November, December, March, and April; smallest differences occurred in May and June. Annually, May and June had the highest mean water levels in all years except 1979 and 1982, and February or March had the lowest levels in all years.

The greatest frequency of high water levels (daily water levels exceeding 3.0 ft at the Oshkosh gage) among years occurred in 1978 ($P < 0.005$) when water levels exceeded 3.0 ft for almost the entire May-July period (Table 7). The lowest frequency of high water days occurred in 1977. Among months, high-water days occurred more frequently during May and June than during other months for all years pooled ($P < 0.005$). May had more high water days than all other months in 7 of 10 years, followed by June with the second highest in 4 years (Table 7). Thus the critical early growth period in May and June for macrophytes consistently had higher water levels of greater frequency than other months in most years of the study. For wildrice, June also encompassed part of the floating-leaf stage when rapidly rising water levels can uproot plants. Lowest water levels coincided with another

Table 6. *Mean monthly water levels for the Upper Winnebago Pool Lakes, measured daily at the Oshkosh gage station, 1975-84.**

	Water Level (ft)											
Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1975	2.0	1.5	1.1	2.0	3.2	3.1	2.7	2.5	2.7	2.4	2.3	2.3
1976	1.6	1.0	1.0	2.7	3.1	3.0	2.5	2.4	2.0	1.8	1.7	1.4
1977	1.2	1.1	1.4	2.7	3.0	2.9	2.8	2.5	2.4	2.7	2.6	2.3
1978	1.9	1.1	0.5	2.5	3.2	3.1	3.1	2.9	3.0	2.5	2.5	2.6
1979	2.1	1.5	1.1	3.5	3.1	2.9	2.9	3.0	2.7	2.4	2.7	2.3
1980	1.7	1.1	0.6	2.1	3.0	3.1	2.9	3.0	2.9	2.4	2.3	2.3
1981	1.9	1.3	1.7	2.7	3.1	3.0	2.9	2.9	2.9	2.8	2.5	2.5
1982	1.8	0.8	0.6	2.4	3.0	2.9	3.0	2.9	2.9	3.0	3.1	2.7
1983	1.8	1.1	1.8	2.2	3.1	3.1	2.9	2.8	3.0	2.9	2.8	2.5
1984	1.5	1.1	1.6	2.0	3.1	3.1	3.0	2.9	–	–	–	–

* Mean water levels differed among years and months, 2-way ANOVA ($P < 0.001$).

Table 7. *Number of days that daily water levels exceeded 3.0 ft during April-September, measured at the Oshkosh gage for the Upper Winnebago Pool Lakes, 1975-84.*

	No. Days							
Year	Apr	May	Jun	Jul	Aug	Sep	Total Days	Chi-square*
1975	0	30	25	1	0	0	56	154
1976	4	27	13	0	0	0	44	105
1977	6	10	0	1	0	0	17	34
1978	11	30	25	30	3	13	112	86
1979	27	22	10	3	13	6	81	58
1980	0	23	18	2	20	8	71	65
1981	13	29	12	8	3	6	71	57
1982	0	12	9	15	9	0	45	33
1983	0	24	21	4	1	10	60	79
1984	0	24	19	10	6	1	60	70
Total	61	231	152	74	55	44	–	–

* In each year, for comparisons among months, $P < 0.001$.

critical period when winter drawdown may have exposed overwintering propagules of some species to damage from freezing temperatures (Beard 1973, Nichols 1974).

Relationship Between Water Levels and Macrophytes. Although water levels varied considerably among months and years, water levels had little discernible impact on abundance of submerged macrophytes and wildrice as evaluated in this study. Annual frequency of occurrence of submerged macrophytes along transect B in Sunset Bay, Lake Butte des Morts, and transect C along the west shore of Lake Poygan (Fig. 2) was not related to annual differences in mean monthly water levels for any month from April-September ($r = 0.20$-0.49, $P = 0.87$-0.33 and $r = 0.65$-0.15, $P = 0.16$-1.00, respectively). Of the 5 relative abundance transects, only transects B and C encountered enough macrophytes to warrant inclusion in these analyses. Further, annual frequency of occurrence of submerged macrophytes along transects B and C was not related to frequency of high water levels (> 3.0 ft at Oshkosh gage) in spring (May-June) and summer (July-August) (B: $r = 0.26$, $P = 0.62$, and $r = 0.56$, $P = 0.32$, respectively; C: $r = -0.09$, $P = 0.51$, and $r = 0.11$, $P = 0.86$, respectively). Lowest frequency of high water levels occurred in 1977 and highest frequency occurred in 1978, yet frequency of occurrence of submerged macrophytes along both transects B and C was similar between these years (22% vs. 23% for transect B and 45% for both years for transect C).

Although high runoff, nutrient loading, and turbidity are apt to accompany abnormally high water levels, a significant relationship between annual abundance of submerged macrophytes (% rake coverage) vs. mean monthly water levels and turbidity for transect C in September ($r^2 = 0.99$, $P = 0.01$) provided the only evidence of this synergistic effect. (For May-August, $r^2 = 0.28$-0.75, $P = 0.61$-0.25.) By September, submerged macrophytes completed most annual growth, and the biological significance of these results seems doubtful. A nearly significant relationship existed for transect B during May ($r^2 = 0.93$, $P = 0.07$), but macrophyte abundance varied directly with turbidity. (For June-September, $r^2 = 0.12$-0.61, $P = 0.83$-0.25.) High water levels and turbidity resulting from excessive runoff likely contributed to the decline of submerged macrophyte beds in the Illinois River Valley (Mills et al. 1966) and in Pool 8 of the Upper Mississippi River in 1978-79 (C. Korschgen, U.S. Fish and Wildl. Serv., pers. comm.).

Magnitude of winter drawdown was inconsistently related to abundance of submerged macrophytes for transects B and C. Minimum winter water levels were not correlated ($r = -0.42$, $P = 0.41$) to frequency of occurrence of submerged macrophytes during the next summer for transect C. A nearly significant negative relationship existed ($r = -0.78$, $P = 0.066$) for transect B, implying that lower winter levels resulted in more submerged macrophytes in Sunset Bay. Winter drawdown reduced abundance of most species of macrophytes on exposed mudflats in Murphy's Flowage, Wisconsin, but several species benefited from this drawdown (Beard 1973). Macrophyte response to winter drawdowns depends on species composition, degree of sediment exposure and drying, and snow cover (Cooke et al. 1986). In general, the magnitude of winter drawdown in the UWPL did not produce exposed mudflats. The Sunset Bay area supported a combination of susceptible and resistant species that could result in variable response depending on magnitude of drawdown.

The consistently high water levels in May and June probably contributed to a lack of strong relationships between seasonal and annual variation in water levels and abundance of submerged macrophytes. High spring levels probably controlled plant abundance more than other components of water levels. In a large southern U.S. reservoir, water levels dictated light availability to submerged macrophytes during the critical growth period of April-May, which in turn determined abundance of submerged macrophytes annually (Peltier and Welch 1970). Furthermore, rake sampling along only 1 transect in each of 2 widely separated locations possibly could not detect the magnitude of variation in submerged macrophyte abundance associated with the magnitude of water level variations encountered in this study. Lastly, daily and monthly water level fluctuations differed to an unknown degree at various sampling locations of Lake Poygan, which were approximately 16-22 miles upstream, from those at the Oshkosh gage station.

Acreage of a wildrice stand in the AMSA (Table 1) was positively correlated with mean monthly water levels in July ($r = 0.90$, $P = 0.04$) and nearly so for August ($r = 0.80$, $P = 0.10$) for 1975-79 (Table 6). No relationship existed for April-June and September ($r = 0.30$-0.40, $P = 0.87$-0.50), but mean monthly water levels varied little among years for May and June. The annual frequency of high water days in July-August also varied directly with annual abundance of wildrice ($r = 0.95$, $P = 0.05$). However, the number of high water days in July-August of 1975-77 ranged only from 0-1 (Table 7). During the critical early growth and floating-leaf stages in May-June, frequency of high water days was not related to wildrice abundance during the same year ($r = -0.30$, $P = 0.62$). These unexpected results appear to contradict other studies that demonstrated greater productivity of seeds (and presumably more vigorous plants) by wildrice in years of slightly decreasing summer water levels (Moyle 1944), such as occurred in 1975-77. Perhaps favorable conditions (few high water days and decreasing summer water levels) in all 3 years led to high seed productivity, which allowed further expansion of the stand in 1978 in spite of unfavorable conditions. Wildrice density then declined in 1979 while stand size remained stable (A. Linde, unpubl. data), probably due to the unfavorable 1978 water levels, which likely drastically reduced seed yields. For several lakes in Minnesota, wildrice and seed production failed on average once every 4 years primarily due to high water levels during June and July (Moyle 1944). This analysis did not examine the effect of rapid water level increases in June, which could determine abundance of wildrice throughout the lake system. Interaction of the affects of water level variation among years and with the many other factors affecting wildrice abundance likely confounded results of this analysis.

Water Level Management. A revised water level management plan implemented in 1981-82 mostly but not fully achieved its 3 main goals of: (1) stabilizing late spring and summer water levels, (2) decreasing extreme flooding in spring, and (3) maintaining higher water levels in fall to prevent freeze-out of adjacent marshes and increase muskrat survival (Append. A).

Mean monthly water levels did not differ significantly ($P > 0.05$) between pre- and post-management periods for any month, but approached significance for October and November ($P = 0.057$ for both months) (Table 8). Small sample sizes contributed to the lack of significant differences in these 2 months with the largest differences between pre-and post-management periods. The plan accomplished the goal of maintaining higher water levels in fall, but did not fully moderate water levels in May-June (Table 8).

However, adherence to the target spring-summer level of 3.0 ft did not reduce water levels in May-June from pre-management years, and increased water levels during July-September over pre-management years. In fact, the target 3.0 level actually raised levels over long-term mean levels for May-August 1938-84 (Fig. 4). Thus, macrophytes already stressed by high water levels were further stressed by this plan's spring-summer target levels.

Table 8. *Comparison of mean monthly water levels measured at the Oshkosh gage, for the Upper Winnebago Pool Lakes prior to (1975-81) and after (1982-84) implementation of a water level management plan.*

	Mean Monthly Water Level (ft)		
Month	1975-81	1982-84	P*
Jan	1.8	1.7	0.494
Feb	1.2	1.0	0.255
Mar	1.0	1.3	0.494
Apr	2.6	2.2	0.172
May	3.1	3.0	0.255
Jun	3.0	3.0	0.820
Jul	2.8	3.0	0.172
Aug	2.7	2.9	0.649
Sep	2.7	3.0	0.111
Oct	2.4	2.9	0.057
Nov	2.4	2.9	0.057
Dec	2.2	2.6	0.107

* Pre- vs. post-management years, Wilcoxon rank sums, df = 6 and df = 2, respectively.

Water Clarity

Water Clarity Parameter Relationships. Turbidity and Secchi transparency measured in conjunction with light availability furnished information on water clarity, the accuracy of these parameters as predictors of the 5% photic zone depth, and the approximate light requirements of submerged macrophytes. Although light availability measurements did not determine exact depth of the 5% photic zone, the regression model based on known physical properties of water provided strong predictive capability for most month and lake combinations ($r^2 > 0.95$ for 11 of 18 regressions, and $r^2 > 0.85$ for all regressions; $P < 0.001$ for all regressions). Other transformations ($\log_e$-$\log_e$, inverse-inverse, square root-square root) yielded lower regression coefficients.

Secchi transparency explained 51% of the variability of 5% photic zone depth in the best of several regression equations using different transformations ($\log_{10}$ photic zone = -0.185 + 1.342 $\log_{10}$ Secchi; $P < 0.001$). Photic zone depths regressed on Secchi transparencies for Lakes Poygan, Winneconne, and Butte des Morts in 1986-87 yielded higher regression coefficients for untransformed data ($r^2 > 0.80$ for each lake and year) than 1975-81 data (R. Kahl, unpubl. data). For adjacent Lake Winnebago in summer 1981, Secchi transparency was strongly related to the 1% photic zone ($r^2 = 0.96$) for untransformed data (Sloey and Brosseau 1981).

Regression equations for the 1% and 5% photic zone depths for the UWPL indicated that these depths approximated 3.5 and 2.3 times Secchi transparency, respectively. However, relationships between Secchi transparency and photic zone depth can vary among years and among sites (R. Kahl, unpubl. data). The relationship between Secchi transparency and the photic zone varied considerably among other studies, but in general the 1% photic zone depth typically was 2.7-3.0 times Secchi transparency (Davis and Brinson 1980). The 1% photic zone in Lake Winnebago during summer 1981 was 1.9 times Secchi transparency (Sloey and Brosseau 1985).

In the best regression equation of several using different transformations, turbidity accounted for only 38% of the variability in photic zone depths (1/photic zone = 0.010 + 0.001 turbidity; $P < 0.001$) for the UWPL during 1975-81. Turbidity better predicted Secchi transparency, explaining 68% of the variability ($\log_{10}$ Secchi = 3.579-0.018 turbidity; $P < 0.001$). An inverse transformation of Secchi transparency regressed on turbidity yielded an $r^2 = 0.975$ for Lake Winnebago in summer 1981 (Sloey and Brosseau 1985). After these authors corrected Secchi transparency for variation due to true color, the latter regression of Secchi transparency on turbidity improved to $r^2 = 0.999$. Contribution by color to variability in Secchi transparency decreased throughout summer, and their data suggested that highest color effects probably occurred in spring due to organic leachate from marshes.

Regression equations relating turbidity to Secchi transparency (inverse and log transformations) for a random sample of Wisconsin lakes accounted for only 33% of the variability in Secchi transparency (Lillie and Mason 1983). For Florida lakes, turbidity explained 71% of the variability in Secchi transparency (cited in Lillie and Mason 1983). Chlorophyll *a* proved the best single predictor of Secchi transparency, explaining 76% and 75% of the variability for Wisconsin and Florida lakes, respectively. Addition of turbidity to the regression equation improved the predictability to only 79% for Wisconsin lakes, and addition of true color and turbidity improved the predictability of Secchi transparency to 89% for Florida lakes. True color did not improve the relationships for Wisconsin lakes, but true color alone accounted for 29% of the variability in Secchi transparency (Lillie and Mason 1983).

Photic Zone Depth. For all months and years pooled, Lake Poygan apparently had the greatest mean photic zone (ANOVA, $P < 0.001$; TSRT, $P < 0.05$) of the 3 UWPL from 1975-81 (overall ANOVA: $P < 0.001$) (Table 9). However, relative differences among lakes varied with month from April to September (significant interaction: $P < 0.001$). Differences among months were not significant ($P = 0.127$). During April, the photic zone extended significantly deeper in Lake Winneconne than Lakes Poygan and Butte des Morts ($P < 0.05$), but no differences existed among lakes during May ($P > 0.05$). During June-September, Lake Poygan apparently had a significantly deeper photic zone than did Lakes Butte des Morts and Winneconne ($P < 0.05$). However, during these months water clarity was measured predominantly within dense beds of submerged macrophytes, which modified and improved water clarity at most sampling sites in Lake Poygan. Extrapolation of these data to lakewide conditions overestimated water clarity for Lake Poygan.

For Lake Butte des Morts, photic zone depth increased from April to May-June, then declined in July-August. Lake Winneconne exhibited an erratic pattern but also experienced a decline in photic zone depth from June to August. Considering the eutrophic nature of these lakes, phytoplankton blooms also should have reduced water clarity during July-August in Lake Poygan. Since submerged macrophytes colonized greater depths in Lake Poygan than in Lake Butte des Morts, Lake Poygan probably had a deeper photic zone but not to the extent indicated from the biased sampling in June-August. Water clarity probably was similar in Lakes Winneconne and Poygan from May-September. Data for mid-lake sites sampled biweekly during 1986-90 indicated that Lakes Poygan and Winneconne had similar water clarity, which was better than in Lake Butte des Morts. Seasonally, all 3 lakes demonstrated decreasing water clarity to a low in July-August, and during 1986-90 had photic zones less than and turbidities greater than during 1975-81 (R. Kahl, unpubl. data).

Turbidity. Turbidity also differed among the 3 UWPL ($P < 0.001$), but not among months ($P = 0.22$); relative differences among lakes were not the same in all months (interaction between lake and month, $P = 0.01$) (Table 9). Lake Poygan apparently had the lowest turbidity ($P < 0.05$) of the 3 lakes during 1975-81. However, sampling-site selection for turbidity incurred the same bias associated

Table 9. *Mean monthly 5% photic zone depths (inches) and turbidity (Jackson Turbidity Units) for the Upper Winnebago Pool Lakes, 1975-81.**

Lake	Apr		May		Jun		Jul		Aug		Sep		Pooled	
	Photic Zone	Turbidity	Photic Zone	Turbidity	Photic Zone	Turbidity	Photic Zone	Turbidity	Photic Zone	Turbidity	Photic Zone	Turbidity	Photic Zone	Turbidity
	B**	A	A	A	A	A	A	A	A	B	A	B	A	B
Poygan	34 (7)	32 (7)	57 (11)	26 (11)	87 (26)	19 (20)	88 (22)	18 (24)	101 (16)	11 (19)	89 (10)	15 (10)	82	18
	A	A	A	A	B	A	B	A	B	A	B	B	B	A
Winneconne	69 (1)	23 (1)	57 (4)	20 (5)	67 (11)	18 (15)	50 (7)	25 (9)	33 (7)	29 (8)	39 (3)	14 (6)	53	25
	B	A	A	A	B	A	B	A	B	A	B	A	B	A
Butte des Morts	42 (6)	29 (7)	62 (21)	26 (22)	58 (29)	24 (29)	38 (30)	27 (37)	36 (32)	37 (33)	29 (19)	24 (20)	44	31

* For a variable number and location of sampling sites (1-4) per day, and a variable number of sampling dates (1-12) per month. Total number of measurements used to compute weighted daily means are given in parentheses. For Lake Poygan, biased sampling within dense submerged macrophyte beds resulted in large photic zones not comparable to lake-wide conditions or to the other 2 lakes for June-August.

** Among lakes, monthly means with the same capital letters are not different, Tukey's studentized range test ($P > 0.05$).

with light availability sampling. As a result, data for Lake Poygan during June-September underestimated turbidity levels lakewide. Mean monthly turbidities generally followed the same trends in water clarity evident from light availability data, and ranged from 11-37 JTUs.

In a random sampling of limnological characteristics for Wisconsin lakes, mean turbidity was 3.1 (SD = 4.6) JTUs and the median was 2.1 JTUs (Lillie and Mason 1983). Only 17% of the measurements exceeded 4 JTUs. Impoundments and shallow lakes (i.e., lakes similar to the Winnebago Pool Lakes) typically had high levels of suspended materials and turbidities. During July-August 1976, turbidity at mid-lake sites in the UWPL averaged 15-17 JTUs (Sloey and Spangler 1977), and during July-August 1981, turbidity at these sites averaged 12-24 JTUs (Sloey and Brosseau 1985). Perhaps these lower turbidities at mid-lake sites in 1976 and 1987 reflected greater water depths with less wave and carp resuspension of sediments. Sampling sites in 1975-81 were generally in shallow, near-shore locations.

Light Requirements of Submerged Macrophytes. Submerged macrophytes in Lakes Poygan and Butte des Morts apparently required 5-10% of surface light during May-June at the maximum depths of colonization. In May-June when most of wildcelery's foliage is at or near the bottom, Lake Poygan's 5% photic zone likely reached a depth of 57-67 inches, and its 10% photic zone likely reached 44-59 inches. Wildcelery colonized a maximum depth of 61 inches along transect C in western Lake Poygan during this period. In Lake Butte des Morts, the 5% photic zone extended to a depth of 58-62 inches and the 10% photic zone extended to a depth of 44-48 inches during May-June. The maximum depth colonized by several species of submerged macrophytes along transect B in Sunset Bay was 53 inches. Measurement of water clarity at numerous sample sites from locations other than the immediate vicinity of transects introduced an unknown amount of error into these comparisons between maximum depth of colonization and photic zone depths. The 10% photic zone from May through late July 1986 more closely approximated the maximum depth of colonization by wildcelery at a planting site in Lake Butte des Morts (Kahl 1987).

For sites in other studies with Secchi transparency less than 8.2 ft (as in the Winnebago Pool Lakes), sago pondweed and wildcelery colonized maximum depths equal to 2.0 and 2.4 times Secchi transparency, respectively (Davis and Brinson 1980). These maximum depth-Secchi transparency relationships would have closely approximated the 5% photic zone depth (2.3 times Secchi transparency) for the UWPL. Secchi transparency proved a good predictor of maximum depth of colonization by submerged macrophytes for a large sample of other water bodies (Canfield et al. 1985, Chambers and Kalff 1985), but considerable variability existed for some lakes and between geographic regions.

The photic zone is typically assumed to extend down to a depth where only 1% of surface light is available for photosynthesis (Davis and Brinson 1980). At this depth, light availability allows just enough photosynthesis to compensate for respiration in lab studies with phytoplankton. In actual field studies of macrophytes, considerable variability was found in percent of surface light available at the maximum depth of rooted submerged macrophytes. Generally, the photic zone for submerged macrophytes (non-charophytes and isoetids) in field studies more closely approximated 5-10% of surface light at maximum depth of colonization (Wilson 1941, Davis and Brinson 1980, Howard-Williams and Liptrot 1980, Barko et al. 1982, Dennison 1987) instead of the 1% required by phytoplankton. However, the photic zone for rooted macrophytes varied from 2% to 16% in other studies (Meyer et al. 1943, Wilson 1941, Bourn 1932). Dissolved color differences among sites could account for some of this variation among studies (Chambers and Prepas 1988). Timing and intensity of sampling, plant species composition, substrate fertility and texture, epiphytic populations (Wetzel and Neckles 1986), and silt deposition on plants (Schiemer 1979) could also account for variability in apparent light requirements among studies.

In particular, species growth strategies and seasonal water clarity patterns will influence interpretation of photic zone depths and light requirements of submerged macrophytes (especially if based on light availability at maximum depth of colonization) for each water body. Light availability at the maximum depth of colonization typically decreases from spring through summer as phytoplankton and epiphyton populations increase, but by June or July, foliage has grown upward into the water column. Light availability at the bottom is probably unimportant to established plants during summer, but light availability at the depth of maximum foliage development probably is critical to growth and reproduction at this time. Thus, light availability measured at the maximum depth of colonization during summer probably underestimates light requirements of plants. Unfortunately, no information is available on plant growth and light availability within this photosynthetically active zone (or macrophyte photic zone), and for seasonal variation in light requirements.

Relationship Between Water Clarity and Submerged Macrophytes. Apparent abundance of submerged macrophytes along relative-abundance transects B and C varied annually (Table 10), but this annual variation had little relationship to annual differences in water clarity. Of the 5 transects, only transect B in Sunset Bay of Lake Butte des Morts and transect C at the west end of Lake Poygan (Fig. 2) encountered enough vegetation for inclusion in the analysis.

Macrophyte frequency of occurrence along transect B was not related to annual changes in spring (May-June) and summer (July-August) photic zone depths and turbidity in the same year nor previous year for Sunset Bay, Lake Butte des Morts ($P > 0.28$) (Table 11). For transect C in Lake Poygan, high turbidity during spring of the previous year may have reduced frequency of occurrence of

Table 11. *Summary of Spearman's rank correlation analyses for annual changes in frequency of occurrence of submerged macrophytes along transects and annual changes in mean spring (Apr-Jun) and summer (Jul-Aug) water clarity, Lakes Butte des Morts and Poygan, 1975-80.*

Independent Variable	Dependent Variable	*r*	*P*	N
Turbidity	**Vegetation**			
Lake Butte des Morts				
Spring, same year	Transect B	-0.03	0.96	6
Summer, same year	Transect B	0.03	0.96	6
Spring, previous year	Transect B	0.20	0.75	5
Summer, previous year	Transect B	0.60	0.28	5
Lake Poygan				
Spring, same year	Transect C	-0.46	0.43	5
Summer, same year	Transect C	-0.35	0.49	6
Spring, previous year	Transect C	-0.95	0.05	4
Summer, previous year	Transect C	-0.36	0.55	5
Photic Zone Depth	**Vegetation**			
Lake Butte des Morts				
Spring, same year	Transect B	0.31	0.54	6
Summer, same year	Transect B	-0.09	0.87	6
Spring, previous year	Transect B	-0.20	0.75	5
Summer, previous year	Transect B	0.30	0.62	5
Lake Poygan				
Spring, same year	Transect C	0.41	0.49	5
Summer, same year	Transect C	0.12	0.82	6
Spring, previous year	Transect C	0.63	0.37	4
Summer, previous year	Transect C	0.36	0.55	5

Table 10. *Rake coverage and frequency of occurrence of submerged macrophytes along 5 transects in the Upper Winnebago Pool Lakes, 1975-80.**

	Lake Butte des Morts						**Lake Winneconne**		**Lake Poygan**	
	Transect A**		**Transect B**		**Transect E**		**Transect D**		**Transect C**	
Year	**Cov.**	**Occ.**	**Cov.**	**Occ.**	**Cov.**	**Occ.**	**Cov.**	**Occ.**	**Cov.**	**Occ.**
1975	0.5	1	4.3	6	–	–	0	0	24.9	43
1976	4.1	8	8.4	15	0.4	0	2.2	2	36.3	61
1977	2.9	4	14.6	22	3.8	6	2.0	3	26.6	45
1978	0	0	16.1	23	1.8	3	2.9	5	28.5	45
1979	–	–	5.3	8	–	–	–	–	23.8	31
1980	–	–	10.2	17	–	–	0	0	20.3	43

* Percent coverage of rake tines and percent frequency of occurrence for 100 plots.

** Water depth ranges along transects: A = 18-37 inches, B = 14-89 inches, E = 21-27 inches, D = 17-84 inches, C = 21-65 inches.

submerged macrophytes ($r = -0.95$, $P = 0.051$). Annual variation in water clarity apparently had no effect on macrophyte abundance in the same year.

This analysis did not investigate the relationship between annual variation in mean rake coverage and water clarity because of the subjectivity of assigning rake coverage classes. For instance, varying structural characteristics among species may affect efficiency of collection by the rake and may affect the appearance of extent of rake coverage thus increasing observer bias. Accuracy of the rake sampling technique was assessed for transects B and C in 1979-80 by comparing rake coverage to wet volume of plants sampled (Table 12). For all data pooled, differences in wet volume existed among the 5 coverage classes ($P < 0.001$); but wet volume did not differ among coverage classes 3-5 (TSRT, $P > 0.05$).

Water clarity data were obtained from many locations other than near transects and the sampling pattern was inconsistent seasonally and annually. Furthermore, the rake sampling technique, especially when based on 1 transect per area and sampled once annually, only detected gross changes in submerged macrophyte abundance. Modest annual differences in water clarity could effect more subtle changes. High turbidity in most years may have determined the long-term maximum depth of submerged macrophytes in the UWPL. Plant beds would expand slowly even in years of slightly better water clarity because suboptimal conditions still existed.

Modest annual changes in water clarity probably effect a continuum of responses over many years by submerged macrophytes, which is complicated by localized water clarity differences, concentrations of carp, excessive wave exposure, sediment composition, and nutrient availability that affect phytoplankton and epiphyton populations. Epiphyte colonization on submerged macrophytes may determine long-term growth and survival by limiting nutrient and gas diffusion and light availability to photosynthetic tissue (Wetzel and Neckles 1986). Nutrient loading from internal sources (Laumer 1977, Sloey and Spangler 1977, Wiersma et al. 1977) may have led to similar epiphyte populations in most years. Since phytoplankton cause most turbidity in the eutrophic UWPL (Sloey 1970, Sloey and Spangler 1977), both phytoplankton and epiphyte communities probably act in concert to govern light availability and long-term abundance of submerged macrophytes.

Table 12. *Mean wet volume of submerged macrophytes among 5 coverage classes of rake samples from transects in Lakes Butte des Morts and Poygan, 1979-80.*

Coverage Class (% rake covered)	No. Rake Samples	Mean Wet Volume (ml)
1-12	103	C* 271
13-37	40	B 1,530
38-62	22	A 3,077
63-87	17	A 3,348
88-100	20	A 3,440

* Means with the same capital letters are not different, Tukey's studentized range test ($P > 0.05$).

Sources of Turbidity

Tributaries. Turbidity differed significantly among the major inlets and outlets (Wolf River at Fremont and Winneconne; Fox River at Omro and Oshkosh) to the UWPL and among months ($P < 0.001$ for both) for May-Aug 1975 and April 1976 (Table 13, Fig. 2). Furthermore, the differences among the major inlets and outlets were not the same in each month (significant interaction between month and site, $P < 0.001$). The Wolf River at Fremont generally had the lowest turbidity, but differences among the other 3 sites varied considerably by month. May-July typically had lower turbidity than April and August for all sites. Total suspended solids (TSS) and organic suspended solids (OSS) also differed significantly among major inlets and outlets ($P < 0.001$ for both) and among months ($P = 0.043$ and $P = 0.01$, respectively) (Table 14). In contrast to turbidity, there was no significant interaction between site and month for TSS and OSS ($P = 0.19$ and $P = 0.22$, respectively). Although the Wolf River at Fremont also generally had the lowest TSS and OSS, differences among sites and months for these parameters did not consistently support differences in turbidity.

For all data pooled, significant relationships were found between TSS and OSS vs. turbidity. However, these parameters only accounted for 65% and 63% of the variability of turbidity ($P < 0.001$). The relationship between turbidity vs. TSS and OSS for the Wolf River-Fremont site ($r^2 = 0.38$, $P < 0.001$; and $r^2 = 0.14$, $P < 0.014$, respectively) was the poorest of the 4 major inlet-outlet locations, indicating that factors contributing to turbidity varied more at this site. For the other 3 locations, $r^2 = 0.52$-0.67 for TSS and $r^2 = 0.54$-0.65 for OSS ($P < 0.001$ for all comparisons).

Mean turbidity of lesser tributaries to Lakes Butte des Morts and Poygan did not differ among months ($P = 0.106$) for all sample dates in 1975-78 and 1981 pooled (Table 15). There were no significant differences between lakes in mean turbidity from lesser tributaries for any month ($P > 0.30$). Spring Brook generally had the highest turbidity (34 JTUs) and Slough Creek had the lowest (9 JTUs) of the 6 tributaries (17-23 JTUs for the other 4; see Fig. 2), but significant differences did not exist among tributaries ($P = 0.082$) for all months pooled. Sample sizes were inadequate to test differences among tributaries by month. Despite this lack of significant differences, higher soil erosion rates in spring conceivably resulted in the generally higher turbidity from tributaries in April-May than in June-July.

In-lake vs. Tributary Sources of Turbidity. Comparison of turbidity data among lesser tributaries pooled by lake, major inlets and outlets, and in-lake sites pooled by lake for a subset of data only for May-August 1975 and April 1976 (the only period that major inlets and outlets were

Table 13. *Mean monthly turbidity for major inlets and outlets, lesser tributaries, and in-lake sources to Lakes Poygan and Butte des Morts, May-August 1975 and April 1976.**

Tributary	Turbidity (JTU)**				
	Apr	May	Jun	Jul	Aug
Lake Poygan					
Major inlet (Wolf R.-Fremont)	B[a] 15 (3)	A 8 (5)	A 9 (4)	A 12 (5)	A 17 (4)
Lesser tributaries	AB 34 (2)	A 44 (3)	A 4 (1)	B 3 (2)	–
In-lake	A 36 (4)	A 32 (3)	–	–	–
Major outlet (Wolf R.-Winneconne)	A 40 (3)	A 11 (5)	A 8 (4)	A 14 (5)	B 25 (4)
Lake Butte des Morts					
Major inlet (Fox R.-Omro)	A 21 (3)	B 15 (5)	A 20 (4)	A 23 (5)	A 41 (4)
Major inlet (Wolf R.-Winneconne)	A 40 (3)	B 11 (5)	A 8 (4)	A 14 (5)	B 25 (4)
Lesser tributaries	–	–	A 9 (2)	A 7 (2)	–
In-lake	A 41 (3)	A 35 (6)	A 12 (4)	A 19 (7)	–
Major outlet (Fox R.-Oshkosh)	A 34 (3)	AB 17 (5)	A 12 (4)	A 17 (5)	B 22 (4)

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* Number in parentheses is the total number of measurements used to calculate weighted daily means each month for a variable number and location of sampling sites (1-3) per day, and variable number of sampling dates (1-5) per month for each source.

** Jackson Turbidity Units.

[a] Within months for each lake, means with the same capital letters are not different, Tukey's multiple range test ($P > 0.05$).

Table 14. *Mean total suspended solids (TSS) and organic suspended solids (OSS) (mg/L) for major inlets and outlets of Lakes Poygan, Winneconne, and Butte des Morts, May-August 1975 and April 1976.**

Site	Apr		May		Jun		Jul		Aug		Pooled	
	TSS	OSS	TSS	OSS	TSS	OSS	TSS	OSS	TSS	OSS	TSS	OSS
Fox R.-Omro	A** 55	AB 15	AB 33	A 13	A 60	A 21	A 49	A 21	A 101	A 38	A 56	A 21
Fox R.-Oshkosh	A 45	AB 12	A 39	AB 10	B 28	B 12	A 37	AB 16	A 36	A 16	AB 36	B 13
Wolf R.-Fremont	A 7	B 2	B 14	B 5	B 21	B 5	A 21	C 8	A 24	A 6	B 18	C 5
Wolf R.-Winneconne	A 62	A 22	AB 21	B 6	B 11	B 5	A 21	BC 11	A 45	A 17	B 27	BC 11

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* For Apr, N = 3; May, N = 5; Jun, N = 4; Jul, N = 5; Aug, N = 4.

** Within months, means with the same capital letters are not different, Tukey's multiple range test ($P > 0.05$).

Table 15. *Mean monthly turbidity contributed by 3 tributaries to Lake Poygan and to Lake Butte des Morts, 1975-78 and 1981.**

	Turbidity (JTU)**				
Lake	**Apr**	**May**	**Jun**	**Jul**	**Pooled**
Poygan[a]	34 (1)	31 (4)	15 (7)	20 (6)	19 (18)
Butte des Morts[b]	29 (4)	32 (5)	21 (10)	19 (6)	24 (25)
Pooled	30 (5)	32 (9)	19 (17)	19 (12)	21 (43)

* No differences existed among months and between lakes, ANOVA and t-test ($P > 0.05$); number in parentheses is total number of measurements used to calculate weighted daily means each month, for a variable number of tributary sampling sites (1-3) per day, and a variable number of sampling dates (1-6) per month.

** Jackson Turbidity Units.

[a] Tributaries: Pine River, Willow Creek, and Pumpkinseed Creek.

[b] Tributaries: Dagett's Creek, Spring Brook, and Slough Creek.

sampled) provided further insight into sources of turbidity and turbid-water flow dynamics (Table 13). Mean in-lake turbidity for Lake Poygan was higher than inflow turbidity from the Wolf River at Fremont but similar to inflow turbidity from the smaller tributaries during April and May. Turbidity in the Wolf River at Fremont differed significantly only from in-lake sites in April (ANOVA, $P = 0.029$; TSRT, $P < 0.05$). Differences among sources were nearly significant in May (ANOVA, $P = 0.072$). In Lake Poygan, water from the Wolf River apparently diluted turbidity from smaller tributaries and in-lake sources during spring.

During April, the Wolf River at Winneconne expelled more turbidity, TSS, and OSS from Lakes Poygan and Winneconne than the Wolf River at Fremont contributed to these lakes (Tables 13, 14). This outflow turbidity simply reflected the relatively high turbidity in Lakes Poygan and Winneconne. During May, outflow turbidity from Lakes Poygan and Winneconne decreased to levels below in-lake and inflow turbidity from smaller tributaries. Lakes Poygan and Winneconne possibly acted as sinks for turbidity from smaller tributaries during May.

All sources for Lake Poygan had relatively low turbidity in June, and no differences were found among sources ($P = 0.51$). Turbidity increased slightly in July for the Wolf River at Fremont and Winneconne, resulting in significantly higher turbidity loadings for these sources than for smaller tributaries ($P = 0.005$). Sampling bias within submerged macrophyte beds prevented assessment of in-lake sources of turbidity for June-August. Outflow turbidity, TSS, and OSS levels of the Wolf River at Winneconne steadily rose from June through August, probably due to increased phytoplankton populations in Lakes Poygan and Winneconne. Meanwhile, inflow turbidity increased more modestly, and TSS and OSS remained similar from June through August for the Wolf River at Fremont. By August, inflows had significantly less turbidity than outflows of the Wolf River (ANOVA, $P = 0.024$; TSRT, $P < 0.05$). Lakes Poygan and Winneconne apparently served as incubation chambers for phytoplankton (Sloey and Spangler 1977), flushing some of this phytoplankton downstream into Lake Butte des Morts, especially in August.

The Wolf River at Winneconne discharged relatively turbid water into Lake Butte des Morts during April (Table 13), but turbidity did not differ significantly for the Wolf River at Winneconne, the Fox River at Omro and Oshkosh, and in-lake sites ($P = 0.29$) during April. TSS and OSS data did not fully support this pattern since the Fox River at Omro transported higher suspended solids loadings than the Fox River at Oshkosh although differences were not significant ($P > 0.05$) (Table 14). Apparently, Lake Butte des Morts accumulated suspended solids, especially inorganic solids, from both the Wolf and Fox rivers in April, which the Fox River outlet did not flush from the system. During May, the 3 major inlet-outlet locations transported relatively low turbidity loads (and suspended solids) compared to in-lake sources of turbidity, but turbidity differed significantly only for both inlets vs. in-lake sites (ANOVA, $P = 0.012$; TSRT, $P < 0.05$).

Increasing turbidity in the Fox River at Omro during June and July tended to contribute more to Lake Butte des Morts turbidity than the Wolf River at Winneconne and lesser tributaries ($P = 0.061$ and $P = 0.131$, respectively). By August, inflow of the Fox River at Omro carried significantly greater turbidity loads than inflow of the Wolf River at Winneconne and outflow of the Fox River at Oshkosh (ANOVA, $P = 0.005$; TSRT, $P < 0.05$). Both TSS and OSS supported this pattern for turbidity during June-August.

However, significant differences in TSS existed only for the inlet of the Fox River at Omro vs. the inlet of the Wolf River at Winneconne and the outlet of the Fox River at Oshkosh during June ($P < 0.05$). For OSS, the Fox River at Omro transported significantly greater loads than the Wolf River at Winneconne during June and July, and the Fox River at Oshkosh during June ($P < 0.05$). Phytoplankton, especially diatoms, caused most turbidity during this period at these locations (Sloey et al. 1976).

In summary, inflow from the Wolf River (measured at Fremont) to Lake Poygan apparently contributed little to in-lake turbidity during May-August 1975 and April 1976. Smaller tributaries in spring, and in-lake sources in spring and summer probably accounted for most of Lake Poygan's turbidity during this period. The Wolf River and lesser tributaries apparently carried low turbidity loads during summer 1975. Internal loading of nutrients from sediments, carp, and freshwater drum probably led to high phytoplankton populations (Sloey and Spangler 1977) in summer.

Spring turbidity in Lake Butte des Morts resulted from Wolf River inflows (measured at Winneconne) in April but not May, and possibly from lesser tributaries and various in-lake sources. The Fox River contributed little turbidity to Lake Butte des Morts during spring. Phytoplankton and nutrient enriched water of the Fox River and in-lake sources contributed most to summer turbidity in Lake Butte des Morts.

In 1972-73, most tributaries to Lake Poygan and major tributaries to Lake Butte des Morts delivered high nutrient loads to these lakes (U.S. Environ. Prot. Agency 1974, 1975). Sediments apparently have become nutrient enriched, and subsequent release (i.e., internal loading) of these nutrients fuels high phytoplankton populations during late spring and summer months (Wiersma et al. 1977).

These conclusions should be considered tentative. All tributaries were not sampled on the same day or in each month. Furthermore, sample sites probably did not adequately represent water quality for all tributaries and in-lake sites. The Wolf River may introduce higher turbidity loads to Lake Poygan than demonstrated at Fremont by accruing heavy turbidity loads along the 10-15 miles from Fremont to Lake Poygan, including additional turbidity from the Rat River Watershed (Fig. 2).

Wave Action. Relatively strong, prevailing easterly winds (R. Kahl, unpubl. data) during spring over the 4-6 mile east-west fetches of these large shallow lakes maximized the potential effects of wave action on turbidity. Mean wind speeds were greater during April ($\bar{x} = 11.7$ mph; $P < 0.05$) than any other month during 1977-82. May and June experienced significantly greater mean monthly wind speeds than July and August ($\bar{x} = 10.3$-10.4 mph and $\bar{x} = 8.7$-8.9 mph, respectively; $P < 0.05$).

Wind-induced wave action accounted for 28% of the variation in the photic zone depth during April-May, but apparently exerted little influence on turbidity and the photic zone at other times (Table 16). Several other regressions of mean daily turbidity and photic zone depth on mean daily wind speed yielded significant results ($P < 0.05$), but wind speed never accounted for more than 14% of the daily variability in turbidity and photic zone depth. However, strong winds reduced the accuracy of water clarity measurements, and often prevented safe access to the UWPL. This effectively limited sample size for days with high wind speeds (range for mean daily wind speed was 5-20 mph). Analyses using maximum wind speed (range 7.0-25.0 mph) and gusts (range 19.0-31.0) did not detect a relationship between high winds and water clarity for the UWPL. However, days with mean and maximum wind speeds exceeding 20 mph occurred infrequently from April through June (only 5-8% of all days, or < 3 days/month) so probably had little effect on water clarity.

Table 16. *Summary of linear regression analyses for water turbidity and photic zone depth vs. daily wind speed parameters, Upper Winnebago Pool Lakes, 1977-82.**

Independent Variable	Dependent Variable	No. Days	r^2	P
Daily Wind Speed	**Daily Turbidity**			
Mean	Mean, all sites	128	0.02	0.08
Mean with gusts	Mean, all sites	128	0.02	0.12
Mean, gusts only	Mean, all sites	33	0.03	0.34
Maximum	Mean, all sites	128	0.03	0.05
Mean, Apr and May	Mean, all sites	21	0.00	0.79
Mean, south wind days	Mean, Sunset Bay	13	0.10	0.30
Mean, east wind days	Mean, West Poygan	12	0.14	0.23
Mean, previous day	Mean, all sites	129	0.00	0.85
Maximum, previous day	Mean, all sites	129	0.00	0.60
Daily Wind Speed	**Daily Photic Zone**			
Mean	Mean, all sites	174	0.03	0.02
Maximum	Mean, all sites	127	0.04	0.02
Mean, Apr and May	Mean, all sites	20	0.28	0.02
Mean, south wind days	Mean, Sunset Bay	14	0.04	0.48
Mean, previous day	Mean, all sites	129	0.01	0.43

* Analyses utilized daily means for all sites sampled each day, thus means are derived from variable numbers and locations of sites.

A delayed response, especially by phytoplankton, to the previous day's winds from resuspension of nutrients or cells and other fine particles was not evident for the UWPL (Table 16). Relatively high turbidity and nutrient availability from other sources in the eutrophic Winnebago Pool Lakes may have obscured the impact of additional input from wave action, or a delayed response occurred more than 1 day later. The confounding effects of phytoplankton blooms that typically occur during calm weather in summer and bias associated with sampling in macrophyte beds during June-August may in part account for the lack of a strong relationship. However, existing vegetative structure to attenuate wave action was minimal in spring. Other important factors confounding or masking the impact of wind-induced turbidity include upland erosion, carp activity, sediment composition, shoreline stabilization, and wave action from motor boat activity.

Other studies on these lakes have concluded that wave action may contribute significantly to turbidity (Laumer 1977, Sloey and Spangler 1977). Wave action can increase turbidity by resuspending bottom sediments and eroding shorelines (Chandler 1942, Chamberlain 1948, Mills et al. 1966, Stern and Stickle 1978) and by augmenting water fertility and phytoplankton populations by resuspending nutrients (Wiersma et al. 1977, Bates and Neafus 1980) and particulate organic matter (Demers et al. 1987).

Even moderate winds on these large, shallow lakes may have resuspended and eroded the more susceptible silt, clay, organic particles, and nutrients that tend to remain in suspension for relatively long periods. Wind velocities of 13.5 mph resuspended particulate organic matter (primarily diatoms), resulting in higher phytoplankton populations in the water column in a Lake Erie bay (Demers et al. 1987). Greater wind speeds contributed little additional turbidity. Maximum wind speeds exceeded 15 mph at the Oshkosh Airport on 42% of all days during April-June. In contrast, winds less than 26 mph had little impact on turbidity in Lake Chautauqua, Illinois, but winds greater than 26 mph produced high levels of turbidity (Jackson and Starrett 1959).

Turbidity Attenuation by Macrophytes. Dense beds of submerged macrophytes apparently altered the microclimate and reduced turbidity within the beds at the west shore of Lake Poygan and the AMSA of Lake Butte des Morts, but a dense, narrow stand of emergent macrophytes in Sunset Bay of Lake Butte des Morts had no effect on turbidity. After plants developed in the dense bed of submerged macrophytes along Lake Poygan's west shore, water clarity improved at the middle and shoreward sites within the bed (Fig. 14a). In the overall 2-way ANOVA ($P < 0.001$) significant differences in the 5% photic zone depth existed among sites ($P < 0.001$) and among 33 sampling dates ($P = 0.002$). The inner site had a significantly deeper photic zone than the middle and outer sites for all dates pooled ($P < 0.05$). Photic zone depths did not differ significantly in any month, but differences among sites steadily increased from virtually no difference in April ($P = 0.68$) to nearly significant differences in July ($P = 0.055$) and August ($P = 0.084$). Unexplainably, turbidity data did not support results of the photic zone analysis (overall 2-way ANOVA: $P < 0.001$; among dates: $P < 0.001$; and among sites: $P = 0.48$). Wildcelery, the dominant species in this area, began growing in early to mid-May, and probably attained maximum biomass in mid-July to early August. Greatest water clarity at the inner site coincided with near maximum to maximum biomass of wildcelery.

A mixed wildrice and submerged macrophyte stand also improved water clarity at 2 protected sites in the AMSA of Lake Butte des Morts during April-September 1978 (Fig. 14b). Significant differences in depth of the 5% photic zone among the outer and 2 protected sites ($P < 0.001$) and among 16 sampling dates ($P < 0.001$) contributed to overall significance of the 2-way ANOVA ($P < 0.001$). The photic zone depth was consistently greater at the protected middle and shoreward sites in all months and led to the significant differences among sites for all dates pooled. Turbidity data followed a similar pattern ($P < 0.001$ for overall 2-way ANOVA, and for comparisons among dates and among sites).

However, a monotypic common reed stand did not improve water clarity at protected sites within and shoreward of the stand in Sunset Bay, Lake Butte des Morts during April-September 1976 (Fig. 14c). The 5% photic zone depth did not differ among an outer, exposed site and 2 sites protected from wave action ($P = 0.25$). Turbidity data further substantiated these results (overall ANOVA, $P < 0.001$; among dates, $P < 0.001$; and among sites, $P = 0.71$).

The common reed stand also had no effect on TSS and OSS ($P = 0.89$ and $P = 0.86$, respectively) for all data pooled. In fact, the shoreward site had slightly higher TSS (12.9 mg/L) than the lakeward site (11.2 mg/L), and OSS was similar for both sites (7.2 vs. 7.4 mg/L). Organic material comprised a greater part of TSS than the inorganic component (57-72% vs. 28-43%) and accounted for more of the variability in turbidity ($r^2 = 0.68$, $P < 0.001$) than TSS ($r^2 = 0.58$, $P < 0.001$) at the common reed sites.

Relatively high OSS around the common reed stand in Sunset Bay indicated that turbidity consisted primarily of phytoplankton and/or suspended organic detritus, possibly from carp activity. Sunset Bay attracted large carp spawning populations in the late 1970s (Otis and Weber 1982). Field notes indicated considerable carp activity throughout spring and summer in Sunset Bay and several other common reed stands during this study. Excessive carp populations were not noted within the 2 dense beds of submerged macrophytes investigated during this study.

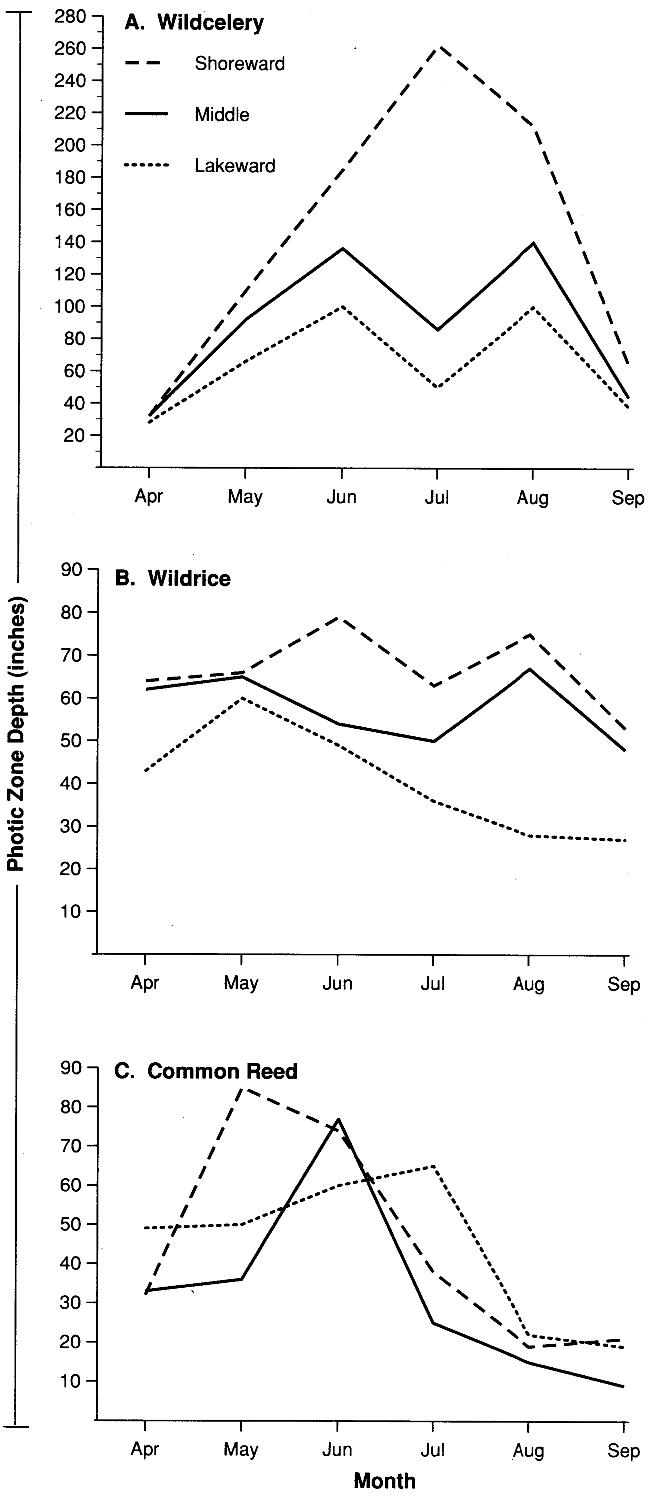


Figure 14. *Mean monthly 5% photic zone depths at exposed sites lakeward of macrophytes and at protected sites in the middle of and shoreward of the macrophytes during 1976-77 for a wildcelery bed along the west shore of Lake Poygan; 1978-79 for a mixed wildrice and submerged macrophyte bed in the Allen's Marsh Study Area, Lake Butte des Morts; and 1975-76 for a common reed stand in Sunset Bay, Lake Butte des Morts (N = 1-7 days/month).*

The other notable difference between the common reed study sites and the wildcelery and wildrice study sites was the lack of dense submerged macrophytes surrounding the protected middle and shoreward sampling sites in the area of the common reed stand. Microclimate modifications attributable primarily to submerged macrophytes likely produced these water clarity improvements by stabilizing bottom sediments and interfering with water circulation, allowing suspended solids, phytoplankton, and nutrients to settle (Stevenson and Confer 1978, Canfield and Jones 1984). Submerged macrophytes produce more underwater foliage than emergent macrophytes and would more effectively alter the microclimate. Shading and lowered water temperature below the submerged macrophyte canopy and macrophyte competition for nutrients likely suppressed phytoplankton populations. Lastly, submerged macrophytes may have produced phytotoxins, further inhibiting phytoplankton blooms (Sloey 1969, Phillips et al. 1978).

The common reed stands apparently did not effectively prevent mixing of nutrient and phytoplankton-rich water outside the bed with water in the bay. Floating tire breakwaters across mouths of 2 coves in an Oklahoma reservoir induced only minor improvements in transparency and turbidity even though these breakwaters reduced wave height by 60-70%. This breakwater design apparently allowed rapid mixing of highly turbid lake water with water in the protected coves (Clady et al. 1979).

Physical Impacts of Waves and Undesirable Fish

A solid-panel barrier appeared to enhance growth and abundance of stiff arrowhead and river bulrush but not the abundance of submerged macrophytes, wildrice, and round-stemmed bulrushes. Dry weight biomass of macrophytes (all species pooled) differed significantly among a solid-panel exclosure, wire-mesh exclosure, and control plot ($P < 0.001$) in the AMSA and among years ($P < 0.001$) from 1975-80. Effects of the protection treatments also deviated among years (significant interaction, $P < 0.001$).

Submerged macrophytes responded differently from emergent forms, partially contributing to the significant interaction and necessitating separate analyses for the 2 groups. Biomass of both submerged and emergent plants differed among treatments ($P < 0.001$ for both) and among years ($P < 0.001$ for both; Table 17). A significant interaction between treatments and years also existed for both submerged and emergent macrophyte analyses ($P < 0.001$ for both).

Submerged macrophytes, primarily wildcelery, dominated the solid-panel exclosure and control plots in late summer 1975. Emergent macrophytes were sparse in both plots (Table 17). Emergent macrophytes were not sampled in 1976. Macrophytes were not sampled in the wire exclosure in either year.

Emergent macrophytes increased in the solid-panel exclosure from 1975 to 1977 ($P < 0.05$) due primarily to rapid growth of stiff arrowhead and river bulrush stands. These species comprised 47% and 26% of total emergent biomass in 1977, respectively. Expanding stands of emergent macrophytes supplanted submerged species, which decreased during the same period in the solid-panel exclosure ($P < 0.05$). Abundance of emergent macrophytes peaked in 1977 and remained stable through 1978 in the solid-panel exclosure.

In contrast, submerged macrophytes in the control plot increased during 1975 to 1977 ($P < 0.05$), but then declined as emergent macrophytes, primarily wildrice, increased from 1977 to 1978 ($P < 0.05$). Wildrice produced about 10 times the biomass in 1978 as in 1977 in the control plot.

Biomass of submerged macrophytes also declined significantly in the wire exclosure from 1977 to 1978 ($P < 0.05$) due to a 77% reduction in water milfoil. Unlike the control plot, the dominant emergents, wildrice and round-stemmed bulrushes, remained stable in the wire exclosure.

Turbidity, TSS, and OSS did not differ ($P > 0.05$) between the exclosure and control plots in 1975-77 (Table 18), and therefore, did not cause differences in submerged macrophytes among these plots. Additionally, changes in

Table 17. *Mean dry weight of submerged and emergent macrophytes in solid-panel and wire mesh exclosures and a control plot in the Allen's Marsh Study Area, Lake Butte des Morts, 1975-80 (N = 20).*

	Mean Dry Weight (g/0.67 ft^2)											
	1975		1976		1977		1978		1979*		1980*	
Treatment	**Sub.**	**Emer.**	**Sub.**	**Emer.**	**Sub.**	**Emer.**	**Sub.**	**Emer.**	**Sub.**	**Emer.**	**Sub.**	**Emer.**
Solid	A** 8.53	A 0.06	A 6.68	–	B 2.56	A 25.96	B 1.05	A 23.31	B 0.44	A 16.40	B 0.47	A 15.16
Wire	–	–	–	–	A 9.54	B 7.14	A 3.50	B 6.94	A 4.63	B 7.20	–	–
Control	B 5.62	A 0.41	A 6.27	–	A 10.23	B 2.36	A 4.50	B 9.45	A 4.97	B 2.32	A 5.81	A 18.57

* Solid and wire structures were removed in April 1979, and plots were sampled late July to mid-August.

** Among treatment and control plots for submerged and emergent macrophytes, means with the same capital letters are not different, Tukey's studentized range test ($P > 0.05$).

Table 18. *Mean turbidity and total suspended solids (TSS) and organic suspended solids (OSS) for solid-panel and wire mesh exclosures and a control plot, Allen's Marsh Study Area, Lake Butte des Morts, 1975-77. Sample size in parentheses.**

	Turbidity (JTU)**				TSS (mg/L)	OSS (mg/L)
Treatment	**1975**	**1976**	**1977**	**Pooled**	**1975**	**1975**
Solid	9 (12)	27 (17)	11 (17)	16 (46)	43 (9)	26 (9)
Wire	10 (10)	30 (15)	11 (15)	18 (40)	29 (14)	15 (14)
Control	12 (12)	28 (15)	11 (18)	17 (45)	22 (13)	11 (12)

* No differences existed among treatments and control plots, ANOVA ($P > 0.05$).
** Jackson Turbidity Units.

abundance of submerged macrophytes in the control plot from 1975-77 did not correspond to varying water turbidity among these years.

After removal of the solid-panel exclosure in April 1979, emergent macrophytes declined during the subsequent 2 growing seasons, producing significantly less biomass in 1980 than 1978 ($P < 0.05$) (Table 17). In particular, the dominant emergents—stiff arrowhead and river bulrush—declined the most from 1978 to 1980. Submerged macrophytes did not respond positively to the decline of emergents in 1979-80.

A relatively large, but non-significant ($P > 0.05$) decrease in wildrice occurred in the control plot from 1978 to 1979. Wildrice then increased from 1979 to 1980 ($P < 0.05$) in the control plot. Submerged macrophytes remained stable from 1978-80 ($P > 0.05$). Abundance of macrophytes in the wire-exclosure plot did not change from 1978 to 1979 for both emergent and submerged macrophytes after removal of the structure in spring 1979 ($P > 0.05$). Macrophytes were not sampled in the wire-exclosure plot in 1980.

Abundance of macrophytes in the vicinity of the exclosures in the AMSA was apparently affected by water level fluctuations, insect infestations, vertebrates, and macrophyte species interactions more than wave action or undesirable fish. Relatively low water levels during each summer from 1975-77 likely contributed to the increased biomass of emergents, primarily stiff arrowhead and river bulrush in the solid-panel exclosure during this period. A similar response by these species was observed during drought conditions in 1988-89 that produced low summer water levels (R. Kahl, pers. obs.). These favorable growing conditions likely led to lakeward expansion and increased density of the wildrice stand in this area each year from 1975-78, accounting for the increasing abundance of emergents (primarily wildrice) in the control plot over the same period. Then high water levels during April-July 1978 probably stressed plants, reducing energy storage in overwintering structures of arrowheads and bulrushes and seed production of wildrice, which reduced biomass in both the solid-panel and control plots in 1979. Relatively late sampling and early senescence of stiff arrowhead and river bulrush further explain the apparent decline in emergent macrophytes in this plot during 1979. However, water level fluctuations do not account for the lack of differences in emergent biomass (primarily wildrice and round-stemmed bulrushes) in the wire exclosure plot from 1977-79. An insect infestation on round-stemmed bulrushes reduced stem density of these species in the AMSA in 1977-79, causing differential mortality throughout the area, especially in the solid-panel exclosure plot, and probably contributed to these inconsistencies.

Possibly the most important factor responsible for the decline in emergents in the solid-panel exclosure plot after removal of the exclosure was grazing by muskrats. By fall 1978, muskrats had built several lodges near the solid-panel exclosure plot. Arrowheads and river bulrush supply food and lodge building material for muskrats (Bellrose 1950, Sather 1958). Muskrats could have grazed these plants after removal of the solid structure. Muskrats severely reduced density of a river bulrush stand in Rice Lake, Nebraska (Sather 1958).

Stiff arrowhead (the dominant emergent species) reportedly tolerates moderate to severe wave action (Harriman 1970), and this species occurred at various sites with greater exposure to severe wave action than the AMSA. Stiff arrowhead stands at exposed, open-water sites in Pool 9 of the Upper Mississippi River attained greater biomass than stands at relatively sheltered, backwater sloughs (Clark and Clay 1985). Of the 5 exclosure sites in the Winnebago Pool Lakes during 1975-80, only this one survived wave and ice action over 4 years due to the relatively sheltered location. Other, more exposed sites in the UWPL supported relatively dense emergent and submerged macrophytes.

For submerged macrophytes in the vicinity of the exclosures in the AMSA, species interaction, especially between submerged and emergent macrophytes, apparently explained changes in abundance in this shallow area with firm sediments more than wave action. In con-

PHOTO: A. LINDE

Muskrats harvested emergent macrophytes for food and to build lodges in 1978-79 near the solid panel exclosure plot (marked by stakes) in the Allen's Marsh Study Area, Lake Butte des Morts. This activity in part explained the decline in emergents after removal of the exclosure in 1978.

trast, wave action over a somewhat greater fetch reduced biomass of sago pondweed and *Potamogeton filiformis* by as much as 80% over the course of a growing season in an English lake (Jupp and Spence 1977). Several other studies utilizing exclosures (Tryon 1954, Robel 1961, King and Hunt 1967) concluded that carp directly destroyed submerged macrophytes by uprooting or grazing. Their wetlands apparently supported higher carp populations.

An exclosure experiment in 2 other locations with firm sediments in the UWPL during 1986 provided little evidence that waves and carp directly reduced biomass of wildcelery (Kahl 1987). However, soft, unconsolidated sediments may allow greater disruption of macrophytes by waves and carp. Furthermore, waves and carp likely contribute more to turbidity in shallow zones with soft sediments.

In general, wave action and undesirable fish had little direct impact on most species of macrophytes in this area. Instead, subtle synergistic impacts of vertebrates (primarily muskrats), water level fluctuations, insects, wave action, and water clarity differentially affected the abundance of the various emergent and submerged forms in the AMSA. Wave action also may affect macrophyte distribution indirectly through sedimentary processes leaving coarse, nutrient-poor sediments at exposed sites (Jupp and Spence 1977).

Insect Infestations in Round-stemmed Bulrushes

In the AMSA, an insect infestation appeared to decrease stand vigor of round-stemmed bulrushes within the solid-panel exclosure and in an adjacent stand during 1977-79. Larvae and pupae of 2 aquatic moth species (Lepidoptera) infested more than half of all stems collected from June-September 1977-79 (Table 19). Discolored stems had higher infestation rates than green stems in 1977 and 1978 but not in 1979. Both green and discolored stems contained an average of about 2 lepidopterans per infested stem in 1977-79. Lepidopteran larvae hollowed stems, causing premature browning and collapse. These data reflect minimum infestation rates

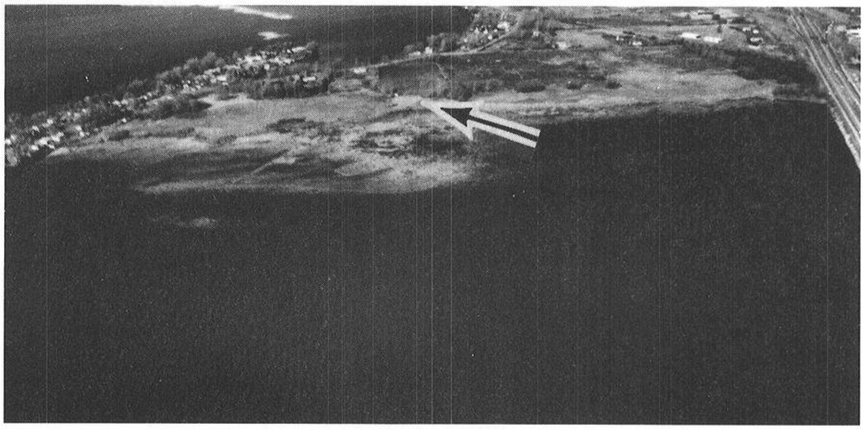


PHOTO A LINDE

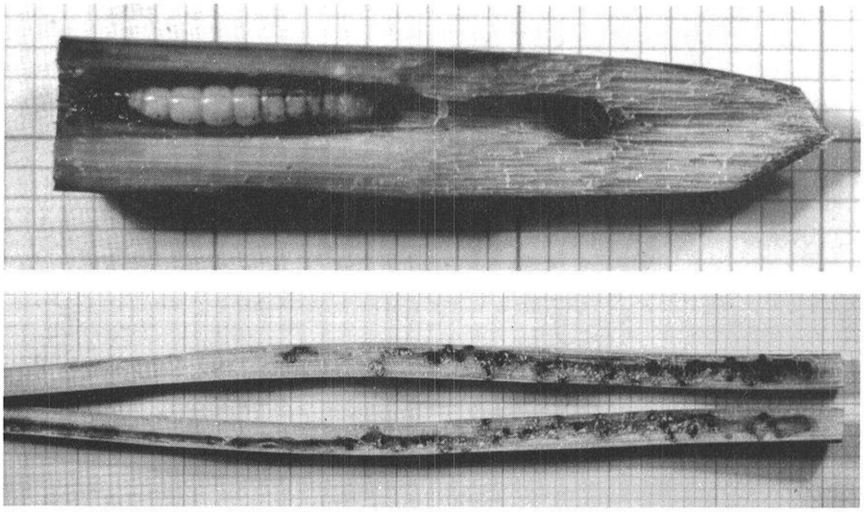
The Allen's Marsh Study Area, Lake Butte des Morts (location of wave and carp exclosures marked by arrow) was relatively protected from west, north, and east winds by Sunset Point to the north-west and by the U.S. Hwy. 41 causeway to the east. (Photo taken facing north.)

Table 19. *Insect infestation of round-stemmed bulrushes, Allen's Marsh Study Area, Lake Butte des Morts, 1977-79.*

Infestation Parameter	1977	1978	1979
No. Stems Examined	48	225	261
Green stems	25	85	128
Discolored stems	23	140	133
Lepidopteran Infestation Rate (%)*	66.0 (30.7)**	62.4 (30.7)	56.8 (22.4)
Green stems	55.7 (30.7)	51.6 (34.2)	62.5 (25.4)
Brown stems	76.3 (22.8)	72.4 (24.4)	51.1 (18.4)
No. Lepidopterans/Infested Stem*	2.2 (1.2)	1.9 (1.0)	1.8 (0.7)
Green stems	2.2 (1.6)	2.1 (1.2)	1.8 (0.9)
Brown stems	2.2 (1.1)	1.8 (0.8)	1.8 (0.5)
No. Hymenoptera/Infested Stem*	0	0.4 (0.6)	0.1 (0.1)
Green stems	0	0.1 (0.4)	0.1 (0.1)
Brown stems	0	0.6 (0.7)	0.2 (0.1)

* Based on daily weighted means from a variable number of days that stems were collected: N = 3 in 1977, 12-13 in 1978, and 11 in 1979.

** Standard deviation in parentheses.



PHOTOS A LINDE

Larvae of 2 aquatic lepidopterans channelized and severely damaged stems of round-stemmed bulrushes in the Allen's Marsh Study Area, Lake Butte des Morts.

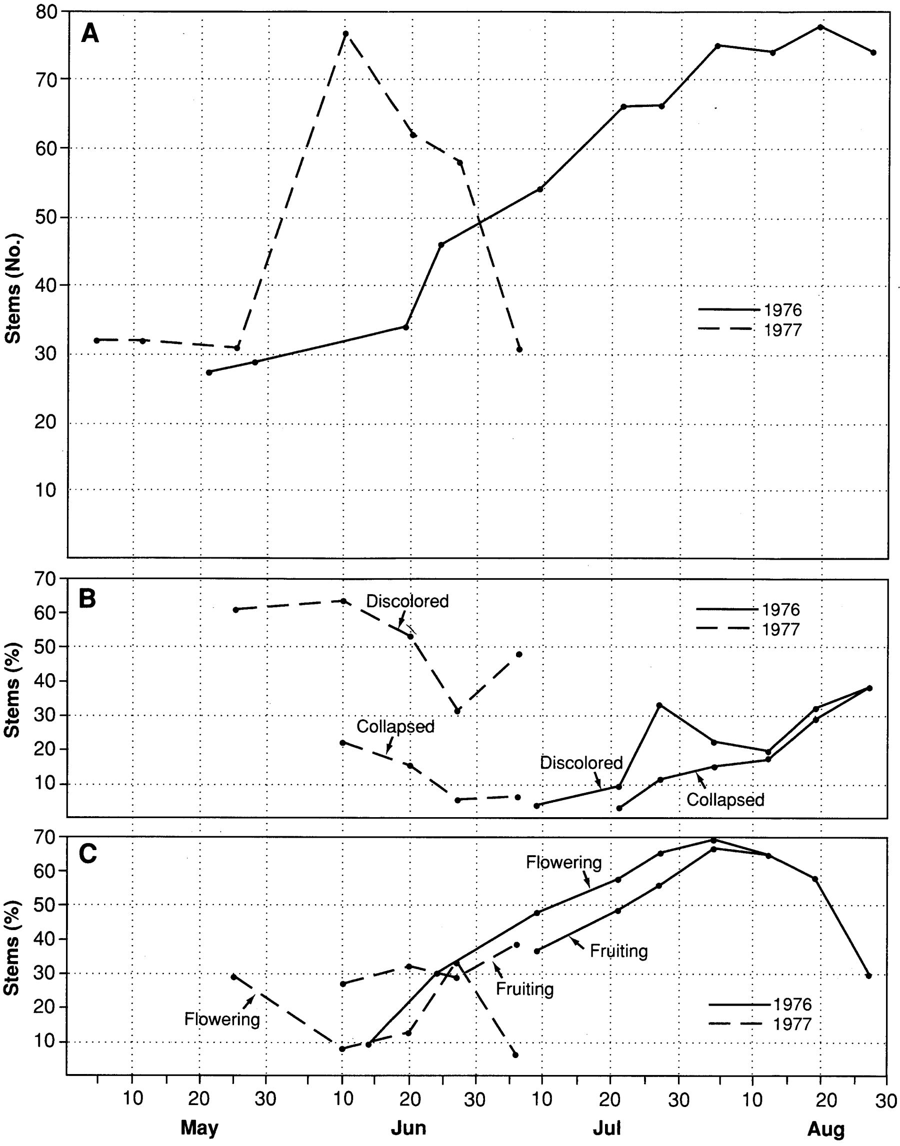


Figure 15. *Stem density (a), phenology of discolored and collapsed stems (b), and phenology of flowering and fruiting (c) for all round-stemmed bulrush stems in a 625 ft² wave and carp barrier at Allen's Marsh Study Area, Lake Butte des Morts, 1976-77.*

because many stems had signs of channelization but no larvae and pupae. Additionally, the most heavily infested stems were not sampled because they had collapsed below the water surface.

Stem density in the solid-panel exclosure increased throughout the 1976 growing season to a maximum of 78 stems in mid-August (Fig. 15a). During 1977, stem density increased to a maximum of 77 stems by mid-June, presumably reflecting the vigorous expansion of the stand apparent in the previous year. However, by late May 1977, many stems had discolored and by late June, many stems had collapsed, greatly reducing stem density by early July (Fig. 15a, 15b). Stems discolored and collapsed much earlier in 1977 than in 1976. Furthermore, stressed plants in the solid-panel exclosure during 1977 initiated and terminated flowering earlier than in 1976, and a lower percentage of stems flowered in 1977 than 1976 (Fig. 15c).

During summers of 1977-80, an adjacent stand of round-stemmed bulrushes supported the highest mean stem density in mid-July 1977 (Fig. 16a). By mid-August, this stand experienced a significant loss of stems (ANOVA, $P = 0.003$; TSRT, $P < 0.05$), and by mid-September, mean stem density declined further, although nonsignificantly (TSRT, $P > 0.05$). This stand produced fewer stems during each of the next 3 years than in 1977, although differences in maximum stem density were not significant ($P = 0.41$). In contrast to 1978-79, stem density during 1980 remained constant from mid-July through mid-September. This lack of a decline in late summer 1980 resulted in nearly significant differences among years for stem density in mid-September ($P = 0.058$).

Annual and seasonal patterns in percentage of collapsed stems in the AMSA supported the conclusion that insect damage caused stem density declines (Fig. 16b). The proportion of collapsed stems was relatively high in 1977-78 as compared to 1979-80, reflecting the major stem losses that occurred in 1977-78. Infestation rates and proportion of collapsed stems appeared to slowly decline from 1977-78 to 1979-80, possibly accounting for the apparent recovery by late summer 1980.

Round-stemmed bulrushes also harbored larvae of an unidentified parasitic wasp, typically attached to lepidopteran larvae, in 1978-79 (Table 19). These larvae occurred in 0%, 38%, and 14% of bulrush stems during 1977, 1978, and 1979, respectively. Apparently, this parasitic wasp quickly responded to the infestation resulting in control and reduction of the lepidopteran population by 1979.

Although the lepidopteran infestation significantly reduced stem density over several years, there was no evidence that insects caused long-term injury to the round-stemmed bulrush stand. Instead, these data indicate that insects can negatively impact macrophytes on a short-term basis. This infestation affected stand vigor by reducing stem density and the rate of flowering, and by altering flowering phenology. Loss of stems for gas transport to rhizomes probably further stressed plants. These events likely reduced energy assimilation rates of rhizomes and formation of buds for subsequent stem production. Severe insect infestations in conjunction with other decimating factors could cause long-term reductions in macrophytes.

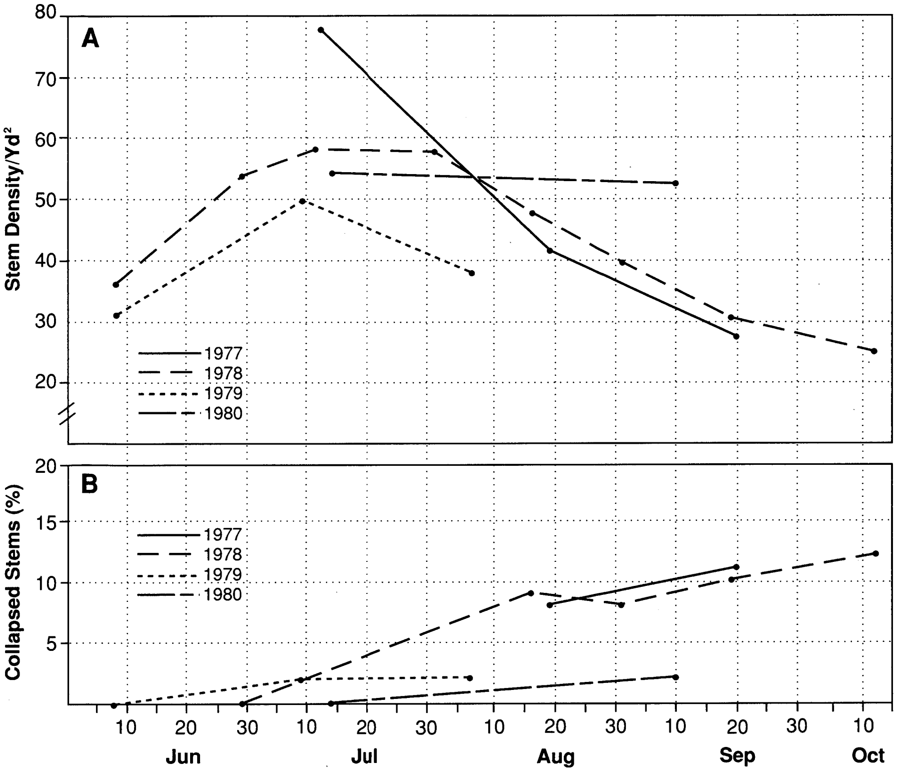


Figure 16. *Density of above surface stems (a) and phenology of collapsed stems (b) of round-stemmed bulrushes at Allen's Marsh Study Area, Lake Butte des Morts, 1977-80 (N = 9-10 systematically located plots of 6.9 ft² in 1977 and 6.4 ft² in 1978-80).*

SUMMARY

History of Macrophyte Changes and Water Level Management

Prior to impoundment in the 1850s, the Upper Winnebago Pool Lakes (UWPL) were naturally eutrophic, large riverine marshes supporting dense emergent macrophytes dominated by wildrice. Subsequent transition of the Winnebago Pool from a riverine marsh ecosystem to a large, turbid, open-water lake system encompassed 3 phases: (1) large-scale formation and disintegration of floating bog after impoundment, (2) replacement of bog by other emergents and submerged macrophytes from the 1930s to the 1950s, and (3) disappearance of those successional macrophytes in the 1960s.

Impoundment increased summer water levels by an average of 2 ft in the 1850s and led to extreme short-term fluctuations, primarily an amplified frequency and magnitude of flooding. This rise probably eliminated emergent macrophytes from the deepest areas and created large expanses of floating bog consisting of wet meadow, lowland prairie, and emergent marsh macrophytes. Wave and ice action later disintegrated floating bog and created small, floating islands of emergent macrophytes that severe flooding readily swept away. Total bog and marsh loss prior to 1961 approximated 5,200 acres on Lake Poygan, 1,500 acres on Lake Winneconne, and 3,800 acres on Lake Butte des Morts. Most of the bog and marsh disappeared prior to 1937.

From the late 1930s to late 1950s, spring and summer water levels continued to fluctuate annually, but the long-term average increased by only 0.5 ft after 1937. However, submerged macrophytes and deep-water species of emergent macrophytes slowly declined through the 1950s. This decline probably was due to stress from long-term high water levels and extreme fluctuations, slowly increasing water depths from continuous erosion of sediments in littoral zones, and slowly increasing turbidity.

Average late-spring and summer water levels did not differ in the 1960s and 1970s from levels in the 1940s and 1950s. However, an accelerated decline in macrophytes in the early to mid-1960s created the large, turbid, open-water lakes evident during the 1970s and 1980s. This rapid decline probably was influenced both by extreme, prolonged flooding (especially in 1960, 1969, and 1973)

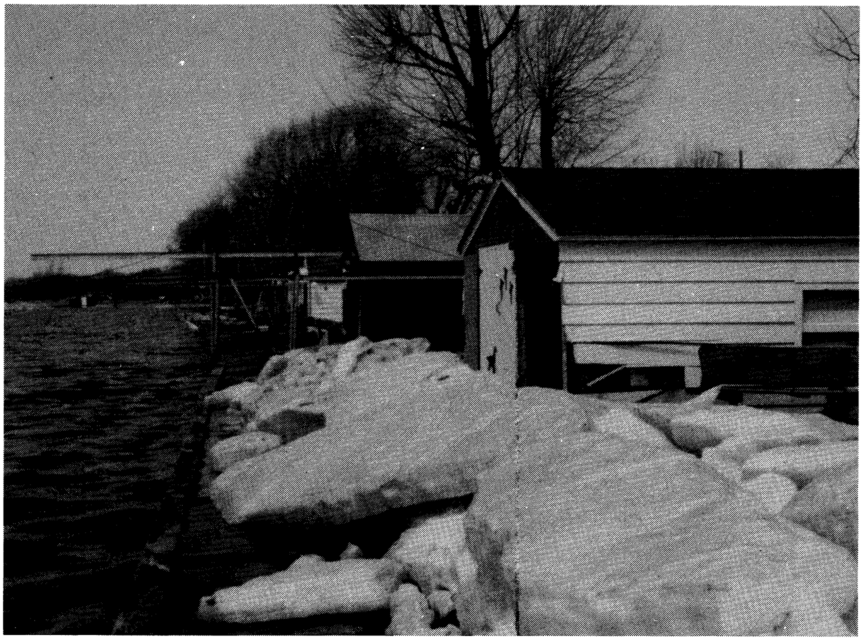


PHOTO: A. LINDE

Ice shoves from rising water levels and strong winds in spring can cause severe damage to marsh edges and shorelines as evidenced by this damage to a boat house in Boom Bay, Lake Poygan.

PHOTO: WINNECONNE HISTORICAL SOCIETY

Impoundment of the Winnebago Pool Lakes in the 1850s created thousands of acres of floating bog that was disintegrated and swept downstream by flooding and wave and ice scour in the late 1800s and early 1900s. This photo shows an estimated 300 acres of bog lodged against the Oshkosh Avenue bridge on the Fox River just downstream from Lake Butte des Morts in spring 1906.

and by increasing water turbidity due to nutrient loading from municipal waste water, agricultural lands, unstable shorelines, lake-shore development, carp and freshwater drum, and wave action. Use of these waters by ducks also declined noticeably during this period.

Ecology of Macrophytes

Wildrice occurred in relatively large stands at 8 sites in Lakes Butte des Morts and Poygan during 1975-79. There were approximately 475 acres of wildrice of mostly sparse to moderate density at these locations in 1976 and 350 acres in 1978. Size and density of wildrice stands varied considerably among the study years and areas.

Common reed was abundant in adjacent marshes and shallow bays, but occurred only at widely distributed sites within the lakes during this study, typically in small, dense monotypic stands. Distribution and density of common reed stands within the lakes remained stable during the past 40 years. The lakes also supported small, widely distributed stands of round-stemmed bulrushes, spike rush, and stiff arrowhead during 1975-82.

Unoccupied habitat for these emergents, consisting of moderate water depths (2-4 ft) with sandy-silty sediments, apparently existed along many shoreline and shoal areas in the 1970s, yet remnant stands of emergents failed to expand or spread. Moreover, bog formation and disintegration in adjacent marshes continued to destroy marsh habitat consisting of common reed and other emergents. Low seed production by common reed and the lack of very shallowly flooded or exposed mud flats for seed germination of most perennial species severely restricted colonization of new areas.

Long-term high water levels (especially consistently high levels during May-June) and fluctuations (primarily rapid rises) likely dictated abundance of emergents on a system-wide basis. The vulnerable floating-leaf stage of wildrice and stiff arrowhead occurred from late May to mid-July when rapid rises in water levels could stress and uproot plants.


PHOTO: A. LINDE

Algae and organic detritus can accumulate on emergent macrophytes such as these round-stemmed bulrushes, breaking and collapsing stems and stressing plants.

Locally excessive algal blooms accumulating on newly emerging stems, carp and waves uprooting and severing new rhizomes and shoots, boating and snowmobiling activity, and insect infestations affected abundance of emergent macrophytes. Round-stemmed bulrushes in late summer and early fall accreted nonstructural carbohydrates, which were utilized in spring and early summer of the following year for rapid growth and initiation of flowering. Damage to stems in June, after the rapid-growth phase and initiation of flowering had reduced energy reserves in rhizomes, likely severely stressed emergent species and caused mortality if damage persisted over several years. Injury to stems after late August likely had minimal impact because rhizomes already had acquired most of the peak energy reserves for winter survival.

Dense emergent stands within the lakes provide living breakwaters, food, cover, and nesting and egg-laying substrates for fish and wildlife, thereby constituting an extremely valuable resource. As such, management of the UWPL should emphasize protection of existing stands and vigorous restoration efforts. Establishing new stands through rhizome or tuber planting is possible, although transplant experiments for common reed were unsuccessful, and techniques need further study. The primary complications were: (1) damage to rhizomes and green shoots from harvest, storage, and planting; (2) deposition of plant material, especially filamentous algae, by waves on new shoots that submerged or severed stems; and (3) interference with elongating horizontal rhizomes by sediment-stabilizing materials, especially tires.

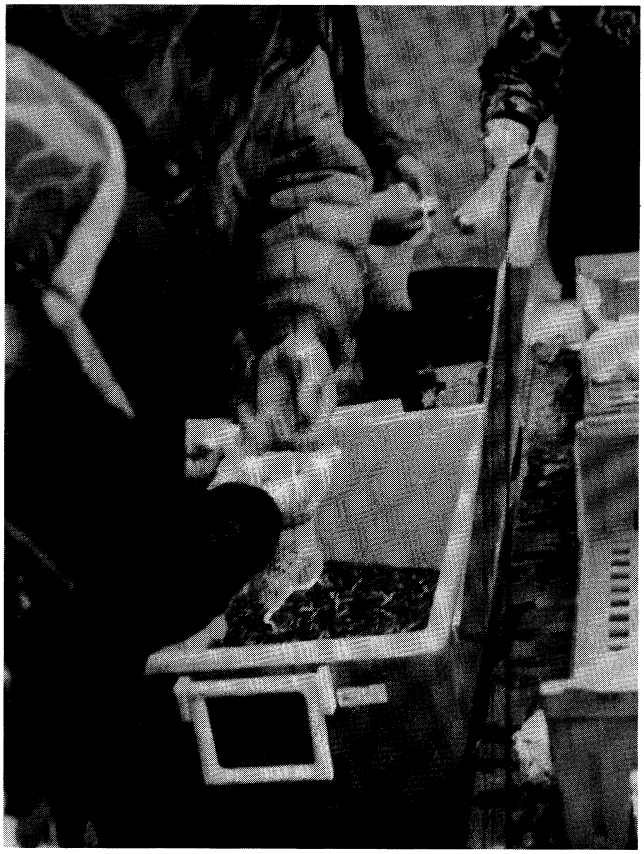
During 1975-79, Lakes Butte des Morts and Poygan supported about 1,650 acres of submerged macrophytes in 8 locations. Lake Winneconne held another 150-200 acres. The abundance of submerged macrophytes remained relatively stable during this period. The commonest species system-wide were coontail, water milfoil, sago pondweed, Canadian waterweed, and wildcelery. Lake Poygan supported the largest submerged macrophyte beds, consisting primarily of wildcelery. Submerged macrophytes grew in maximum water depths of 47-53 inches in Lake Butte des Morts, 51-55 inches in Lake Winneconne, and 55-61 inches in Lake Poygan during the summers of 1975-80. Lake Poygan supported more submerged macrophytes than Lake Butte des Morts due primarily to greater water clarity. Lake Poygan apparently had more submerged macrophytes in 1975-80 than in 1969, indicating an improvement in habitat conditions.

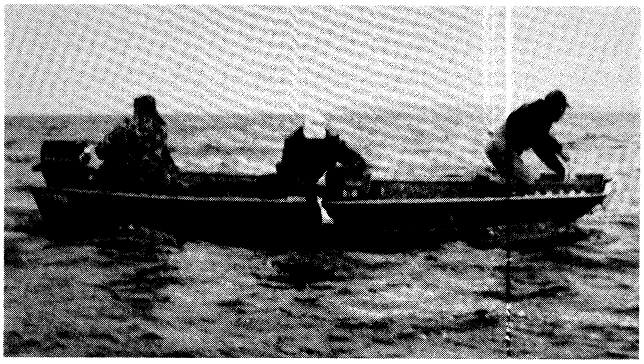
Low light availability probably limited submerged macrophyte growth system-wide. Site-specific factors that influenced water clarity and thus impacted these species likely included carp spawning and feeding, erosion of unstable marsh edge and shorelines, resuspension of soft organic sediments by waves, and turbid inflow from tributary streams. Sago pondweed and wildcelery should be used to reestablish submerged macrophyte beds in the lakes due to their apparent tolerance to turbidity.

Factors Affecting Macrophyte Abundance

Annual fluctuations in water levels had little discernible impact on abundance of submerged macrophytes and wildrice. However, consistently high levels in May and June probably controlled plant abundance more than other components of water level fluctuations.

Water clarity probably controlled the abundance of submerged macrophytes system-wide, although the annual changes in abundance of submerged macrophytes detectable in this study were not related to annual variations in water clarity. The maximum depth of colonization approximated a May-June photic zone depth of 5% in Lake Poygan (57-67 inches) and 5-10% in Lake Butte des Morts (46-60 inches). Submerged macrophytes in the UWPL, therefore, required 5-10% of surface light during May-June. The 5% photic zone depth equaled about 2.3 times Secchi transparency. While Lake Poygan had better water clarity than Lake Butte des Morts, all





PHOTOS: AUTHOR

Wildcelery winter buds can be transplanted by harvesting them with a hydraulic dredge (top), packaging the buds in poly-cotton mesh bags with gravel as a weight (middle), and quickly dropping the bags into the planting area (bottom).

UWPL had high turbidity compared to other Wisconsin lakes. Prevailing high turbidity and epiphytic communities in most years probably dictated long-term abundance of submerged macrophytes.

Inflow from the Wolf River to Lake Poygan apparently contributed little to in-lake turbidity during May-August 1975 and April 1976. Smaller tributaries in spring and in-lake sources in spring and summer probably accounted for most of Lake Poygan's turbidity during this period. Spring turbidity in Lake Butte des Morts resulted from Wolf River inflows in April but not in May, and possibly from lesser tributaries and in-lake sources. The Fox River contributed little turbidity to Lake Butte des Morts during spring. Phytoplankton and suspended solids from the Fox River and in-lake sources contributed most to summer turbidity in Lake Butte des Morts. Sediments in these lakes apparently have become nutrient enriched, and subsequent release of the nutrients fueled high phytoplankton populations in late spring and summer months. Winds contributed to turbidity during spring by resuspending and eroding the more susceptible silt, clay, organic particles, and nutrients that tend to remain in suspension for long periods.

Dense beds of submerged macrophytes apparently altered the microclimate and reduced turbidity within the beds on the west shore of Lake Poygan and at the Allen's Marsh Study Area (AMSA) in Lake Butte des Morts. A dense, narrow, stand of emergent macrophytes in Sunset Bay of Lake Butte des Morts had no effect on turbidity, which consisted primarily of phytoplankton and suspended organic detritus, possibly from carp activity. The microclimate modifications attributed to submerged macrophytes likely produced water clarity improvements by stabilizing bottom sediments, interfering with water circulation, and competing for nutrients.

A solid-panel exclosure at the AMSA appeared to enhance growth and abundance of stiff arrowhead and river bulrush, but not the abundance of submerged macrophytes, wildrice, and round-stemmed bulrushes. In general, wave action and undesirable fish had little direct impact on most species of macrophytes in the AMSA. Instead, subtle synergistic impacts of vertebrates, water level fluctuations, insects, wave action, and water clarity differentially affected the abundance of various emergent and submerged macrophytes. Possibly the most important factor responsible for a decline in emergents after removal of the solid-panel exclosure was grazing by muskrats. Wave action also may affect macrophyte distribution indirectly through sedimentary processes leaving coarse, nutrient-poor sediments at exposed sites.

In the AMSA, an infestation by 2 aquatic moth species decreased the vigor of round-stemmed bulrushes during 1977-79. Moth larvae and pupae infested more than half of all stems collected from June-September in this period. This infestation reduced stem density and the rate of flowering, and altered flowering phenology. Although there was no evidence that insects caused long-term injury to the round-stemmed bulrush stand, insect damage could stress plants enough that they would succumb to other adverse factors.

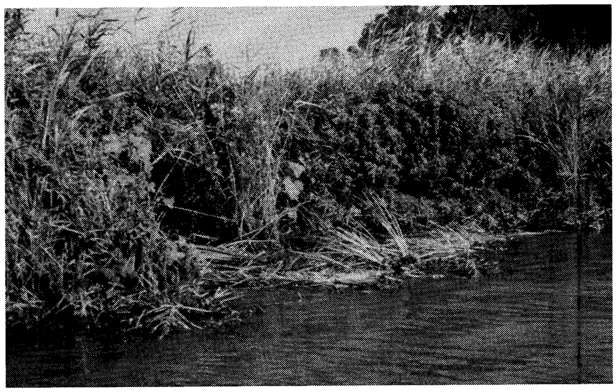
MANAGEMENT IMPLICATIONS AND SPECULATION

Large, shallow lakes such as the Upper Winnebago Pool Lakes (UWPL) comprise a unique and valuable natural resource in Wisconsin offering tremendous management potential. These lakes warrant intensive research and monitoring to further define the scope and impact of all detracting factors and the benefits of management actions. Furthermore, the size and complexity of these systems dictate a multidisciplinary, ecosystem approach to management. The DNR has developed a Winnebago Comprehensive Management Plan to achieve multidisciplinary resource management for the Winnebago system (Wis. Dep. Nat. Resour. 1989). Many of the management recommendations presented below simply reiterate several management proposals included in the plan. This Comprehensive Management Plan could provide the framework for similar efforts to manage other large, shallow lakes in Wisconsin.

1. Continuing decline of macrophytes and riparian marsh poses the central dilemma to managing the UWPL for fish and wildlife resources. Meanwhile large areas of potential habitat remain uncolonized by macrophytes. Rate of macrophyte and marsh loss has decreased in recent years, but deterioration will continue without intensive management efforts. Revision of the water level management plan for the Winnebago Pool Lakes to reduce spring and summer water levels provides the most effective management tool for increasing macrophytes system-wide. Furthermore, watershed and lake management plans must be implemented to control water turbidity. Large littoral zones may also require protection from the physical impact of waves, boats, and undesirable fish, and these areas may need isolation from the influence of turbid inflow from tributaries.

2. The water level management plan implemented in 1982 failed to reduce late spring and summer water levels from the long-term average. Consistently high water levels in May-June during all years of the study likely controlled abundance of emergent macrophytes and in concert with high turbidity determined abundance of submerged macrophytes, and likely accounted for the lack of a relationship between seasonal and annual variation in water levels and abundance of macrophytes.

   Lower spring-summer water levels, especially during the critical growth period from late April through June, would increase sediment temperatures and light availability which encourage earlier and faster growth, and might allow plants to shunt more energy into vegetative reproduction and production of more overwinter propagules with larger energy stores. Rapid increases in water levels after mid-April must be avoided by better anticipation of water level rises from runoff and precipitation events and quicker response time by dam operators. Elimination of these fluctuations in early summer prevents uprooting of plants in the floating-leaf stage and, in later summer, prevents stress to plants that are flowering and producing vegetative propagules. Very high water of long duration in 1 year could greatly reduce the abundance of macrophytes for many years. Due to relatively poor water clarity and moderately high water levels (under existing water level management) during subsequent years, expansion at outer margins of remnant macrophyte beds and re-colonization in new locations would proceed slowly if at all.



PHOTOS: A. LINDE

Strong wind storms can resuspend sediments and erode shorelines causing turbid waters and damaging shorelines and riparian marshes.

3. Seasonal and long-term water level fluctuations should be viewed as an integral component of natural wetlands. These fluctuations contribute to healthy, diverse, and dynamic macrophyte communities. Impoundment of wetlands to create large, shallow reservoirs such as the Winnebago Pool drastically disrupts this natural hydrologic regime. After impoundment of the Winnebago Pool, long-term average water levels during spring and summer increased 2.5 feet, and levels were maintained as closely as possible to this new target level. Although water levels oscillated widely about this target level from year to year, fluctuations below target levels were dampened and those above target levels were often magnified. Short-term seasonal and annual

fluctuations below target levels were typically reduced due to conservative water level management resulting from social, political, and economic pressures to maintain relatively high but constant levels. This reduced and often eliminated the drought portion of the natural hydrologic cycle. Meanwhile, short-term fluctuations above target levels often were amplified above natural fluctuations after major snowmelt and precipitation events. Impoundment and agricultural/residential development throughout the watershed eliminated most wetlands and much of the vegetation that stored and slowed runoff, buffering the pool from extreme flooding. These changes increased the magnitude and rapidity of runoff, leading to excessive flooding that was heightened by the constricted outflow at the dam and often slow response by dam operators to runoff events.

Spring and summer water levels have essentially been maintained at flood stage with drastic curtailment of the drought phase of the natural hydrologic cycle. Thus revision of the water level management plan provides one of the most effective alternatives to restore macrophyte communities. The revised plan should maintain lower average spring-summer water levels and incorporate periodic partial drawdowns throughout 2-3 growing seasons to simulate drought conditions. Occasional fluctuations above this lower target level that simulate flood conditions likely will continue to occur and are as necessary to healthy macrophyte communities as drawdowns. However, these flood stages need to be moderated.

4. Target spring-summer water levels should be reduced by at least 0.5-0.75 ft (from 3.0 ft to 2.25-2.50 ft) at the Oshkosh gage, and be allowed to fluctuate above and below this level in a manner reflecting natural seasonal and annual precipitation and run-off patterns. The impact of lower spring-summer water levels on users of the lakes and on macrophytes requires further evaluation and close monitoring. Strategies should be developed to mitigate any negative impacts of lower water levels on users, such as dredging and maintaining important boating channels. Models that predict system-wide changes in water levels, water depths, macrophytes, and area of the lake bottom within the photic zone should be developed and tested before drastic reductions in water levels.

5. This study did not fully evaluate the effects of winter drawdown on macrophytes; other studies demonstrated a negative impact on some species and a positive impact on others when drawdowns exposed mudflats. Thus, magnitude of winter drawdown should be re-assessed and possibly moderated. Normally, winter drawdown occurs after formation of a thick ice cover, which may insulate propagules from harmful freezing temperatures. When ice cover is inadequate, propagules on exposed mud flats may succumb to frost damage, especially if warm weather in early spring breaks dormancy of these propagules. The extent of ice formation in sediments and effects on macrophytes require further evaluation.

6. Water clarity probably is the most important agent affecting abundance of submerged macrophytes system-wide, as concluded in many other studies elsewhere. Although this study did not demonstrate a direct relationship between annual changes in abundance of submerged macrophytes and water clarity, the relatively low annual variability in turbidity probably effected more subtle changes in submerged macrophyte abundance than detectable in this study.

7. Varying maximum depth colonized by submerged macrophytes throughout the system and absence of vegetation in some shallow areas suggest that undesirable fish, wave action, shoreline erosion, lakeshore developments, sediment texture and fertility, and turbid inflow from nearby tributaries are also important locally. Of most importance, these site-specific factors alter water clarity and nutrient availability to phytoplankton and epiphyton. Both phytoplankton and epiphyton communities govern availability of light to submerged macrophytes and ultimately the abundance of macrophytes (Phillips et al. 1978, Wetzel and Neckles 1986). The relationships among seasonal water clarity, light availability, submerged macrophyte light requirements, and maximum depths of colonization remain unclear and require more intensive investigation and long-term monitoring. Both quantity and quality of light (i.e., water clarity and color) should be monitored. These data would allow refinement of management goals and strategies for improving water clarity and even water levels by better defining the maximum depths colonizable by submerged macrophytes.

8. Reducing turbidity requires the development and implementation of watershed and lake management plans (for details of generalized plans for large shallow lakes, see Kahl (1991) and Wis. Dep. Nat. Resour. (1989). Delineation of the most effective strategies requires more research to supplement the limited data from this study and confirm its tentative conclusions. Specifically, future research must better assess major sources of turbidity and nutrients, including contribution by all watersheds, undesirable fish, wave action, sediments, and shoreline erosion and developments. These limited data demonstrate the need for more intensive monitoring of water clarity, dissolved color, total suspended solids (TSS), organic suspended solids (OSS), chlorophylls, and nutrients by all tributaries to the UWPL in conjunction with in-lake sampling. Magnitude and timing of major precipitation events and spring runoff probably dictate nonpoint pollution levels in the watersheds of the Winnebago Pool; thus water quality sampling must encompass several years and include runoff-event sampling.

9. Although this study provided little evidence that waves and undesirable fish physically injured macrophytes in a moderately protected site with firm sediments, wave action probably influences macrophyte distribution and abundance through a variety of subtle synergistic processes. Wave action continues to erode lakeward edges of riparian marshes. Waves and carp probably damage and uproot plants occasionally, especially young plants at exposed sites and sites with soft sediments. However, wave action and carp likely exert the greatest influence on macrophytes by increasing turbidity and algae through resuspension of bottom sediments, erosion of shorelines and marsh edges, and recycling nutrients to algae. Waves then can deposit algae and detritus on plants, submerging or severing them. Erosion and deposition of sediments by waves in part determines macrophyte distribution by altering water depths and sediment composition. Lastly, other detrimental factors such as insects, carp, muskrats and water level fluctuations can increase macrophyte vulnerability to wave action. Circumstantial evidence from this study indicated that carp, waves, and boats injured and severed young shoots and stems of emergents. Severest damage likely occurred along the outer margins of stands and edges of openings within stands. This damage could curtail bud formation and rhizome elongation at the terminal portion of existing rhizomes, thus restricting expansion of these stands and possibly reducing stand density. Uncertainty about the magnitude and effect of these factors requires further investigation. In particular, the extent of indirect effects of wave action and undesirable fish on nutrient availability remain largely unknown. Population status and ecological role of both carp and freshwater drum must be delineated for the UWPL. Excessive freshwater drum populations could affect water clarity more than carp or waves through nutrient recycling to phytoplankton.

10. Due to the variety of potentially harmful impacts of wave action, breakwaters should be an integral part of any management plan for the UWPL. These structures not only can reduce turbidity from resuspension and erosion of sediments and shorelines, but also can redirect turbid flows from tributaries past critical bay and littoral zone areas. Turbid water from tributaries, especially the Fox and Wolf rivers emptying into Lake Butte des Morts, presently disperses over large, shallow delta and bay areas and, in part, limits abundance of macrophytes in these areas. Historically, better defined river channels transported these turbid flows much farther out into the lakes and past these large littoral zones. Shoaling behind breakwaters could decrease water depths and accumulate nutrient-enriched sediments. Breakwaters would also intercept algae and other debris, preventing submergence and injury to plant stems.

    Breakwaters placed in front of unstable shoreline and marsh-edge zones would not only protect these areas, but also create additional area for marsh expansion. In contrast, rip-rapping along shorelines and marsh edges restricts future expansion of marsh habitat. Rock rip-rap breakwaters are the most promising technique, but others include temporary breakwaters, constructed islands, and living breakwaters (Sloey and Spangler 1977) comprised of resistant emergent macrophytes such as common reed, round-stemmed bulrushes, and spike rush. However, the last 3 alternatives, especially temporary breakwaters, have greater drawbacks associated with high maintenance costs, low impediment to interchange of turbid water, and ephemeral benefits than permanent, solid breakwaters.

    Rip-rapped breakwaters have lower esthetics value, but presumably provide the most effective alternative for reducing turbidity through better wave attenuation and barrier characteristics that interfere with mixing of turbid tributary and lake water. Barrier stands of common reed partially protecting Sunset Bay, Lake Butte des Morts, did not reduce turbidity shoreward of the stands. Instead, these stands may have created carp spawning and feeding habitat, which negated any water quality benefits of the living breakwater. Rip-rapped breakwaters could also create carp habitat. Breakwaters should enclose most or all of large littoral zones or bays and should provide sparsely located, small gaps for boat access. This reduces interchange of turbid lake water with water inside the breakwater. Breakwaters and islands would also provide nesting habitat for waterbirds and fish habitat in adjacent shoals. These theorized benefits of breakwaters must be confirmed through a thorough assessment which would also provide greater insight into system-wide impacts of wave action. Evaluations of breakwater projects should minimally include frequent monitoring of water clarity, nutrients, phytoplankton populations, macrophyte populations, carp populations, water depths, and sediment composition prior to and after breakwater construction.

11. Active management of macrophyte and carp populations likely would enhance the success of breakwater projects. The introduction and spread of undesirable plant species or the development of large carp spawning and feeding populations may require control strategies. Rapid reestablishment of desirable macrophytes likely will require a transplant program, especially for emergents that depend on vegetative propagation in submerged situations. Even in areas with existing scattered beds of desirable submerged species, large-scale plantings of submerged macrophytes could produce quicker and more dramatic improvements in water clarity by stabilizing bottom sediments, tying up nutrients, and inducing settling of suspended solids, phytoplankton, and nutrients.

12. Future research must evaluate transplanting techniques for macrophytes. Species recommended for transplanting include common reed, round-stemmed bulrushes, spike rush and stiff arrowhead for their apparent tolerance of moderate water depths (3.5-4.5 ft) and moderate to severe wave action. Attempts to re-establish submerged macrophytes in uncolonized areas of the Winnebago Pool Lakes to improve water, fish, and wildlife resources should utilize sago pondweed and wildcelery due to their apparent tolerance of turbidity. Both of these species also provide important waterfowl foods (Cottam 1939, Martin and Uhler 1939, Anderson and Low 1976, Korschgen et al. 1988). Sago pondweed should be transplanted immediately after ice-out, whereas wildcelery planting can be delayed several weeks. Propagules of all of the above species should be harvested from nearby healthy habitats with water depths similar to the planting site.

    Based on limited information, rhizomes of common reed, bulrushes (hardstem bulrush tolerates deeper water than other *Scirpus* species) and spike rushes should be harvested in early spring before new growth, separated into 8-inch sections with 3-4 buds on each (Haslam 1969*b*), and planted by burying them 2-4 inches deep depending on sediment texture, at water depths of 1-3 ft. A local commercial wildlife plant nursery recommends transplanting these species by planting 1-4-inch rhizomes (depending on species) with several sprouts pushed into sediments just far enough to leave sprouts exposed, at a density of 1 rhizome per yd^2. Plantings should be protected by a breakwater until established. Wildcelery, sago pondweed, and arrowhead tubers should also be harvested in early spring and planted by enclosing them in biodegradable mesh bags (3/bag) with gravel as a weight, then simply dropping the bags from a boat over the planting area in water depths of 1-4 ft at densities of at least 1 bag/yd^2. However, arrowhead tubers may also require being buried in sediments.

13. Ecology, habitat requirements, and factors affecting the distribution and abundance of macrophyte species important in the UWPL require further investigation to ensure selection of the most effective management strategies. Management of macrophytes, especially common reed, in the UWPL also requires a public-awareness campaign about the potential damage posed by boats and snowmobiles.

APPENDIXES

Appendix A. Ecological Goals for the Winnebago Pool, 1980[1]

1. **Begin Winter Draw-down.** Begin at the time of lake freeze-up so that the marshes have time to develop a 6 inch ice cover (to be determined by the DNR) to protect muskrat populations in the adjacent marshes from draw-down. Marshes will freeze over before the lakes do; therefore, an adequate ice cover (about 6 inches) should be present by the time the water is removed from them. Muskrats can continue to live beneath an ice cover even with the water removed.

    The range of freeze-up dates spans November and December. Water levels should be down to spillway level as near to December 31st as physically possible to assure that water is being removed from the marshes at a desirable rate.

2. **Maximum Winter Draw-down.** This should be accomplished by about March 1st to achieve adequate pool drainage. The pool should be drawn down to 12-18 inches below the Menasha spillway crest, contingent on runoff conditions (snow pack and rain). If conditions for probable heavy spring flows exist, it could be reduced to the lower legal limit of 18 inches below the spillway crest. An adequate draw-down will provide the needed storage required to accommodate heavy spring flows during the spring break-up period and reduce flooding. High water levels at and before ice-out on the lakes can cause extensive ice damage to shorelines and marshes.

3. **Spring Water Levels.** Contingent on runoff conditions (snow pack and rain would be deterring factors), hold water levels at draw-down stage until ice-out occurs on Lake Winnebago, at which time the pool can be refilled to a level of about 3.0 ft (16 inches above the spillway crest). A water level of 3.0 ft provides a 0.45 foot leeway to reduce the chance that the upper legal limit of 3.45 ft (21¼ inches above the spillway crest) is exceeded because of unexpected heavy inflows during prolonged periods of heavy precipitation. Ice-out occurs over a wide range of dates.

4. **Late Spring Water Levels.** When precipitation permits, the targeted pool level of 3.0 feet (16 inches above spillway crest) should be achieved no later than June 1st to prevent damage to wild rice by rising water levels. During June, wild rice is in the critical floating leaf stage and is easily uprooted by rising water.

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[1] Written in August 1980 by the Wisconsin Department of Natural Resources Fox-Wolf Lakes Task Force, with Arlyn Linde as primary author.

However, if the 3.0 foot level is not reached by June 1, the pool should continue to be filled in an attempt to attain the 3.0 foot level to assure adequate storage for the summer period.

5. **Summer Water Levels.** Hold water levels at or near 3.0 feet through most of the summer which will allow for a slight decline during the period of maximum evapotranspiration loss beginning in July. The rationale here is that this level would offset the frequency of sudden rises in water level during this period, decreasing the potential damage to marsh substrate and associated aquatic vegetation.

   Where desirable, water levels may be allowed to fluctuate near the 3.0 foot level in late summer to achieve continued near-normal flow.

Conclusion

The most critical period for maintaining aquatic vegetation stands in the upper Fox-Wolf Lakes is in the early spring when high water and ice action have destroyed large tracts of marshland and extensively damaged shorelines and improvements in the past. This proposal aims at reducing the chance for similar damage to occur in the future.

The goals are based on studies, discussions, and meetings (particularly one on March 11, 1980) by State (Wisconsin Department of Natural Resources and Fox Valley Water Quality Planning Agency) and Federal (Corps of Engineers, Fish and Wildlife Service, and the Geological Survey) agencies over the past several years. These are summarized in a letter of August 27, 1980 from Andrew C. Damon, Deputy Secretary, Wisconsin Department of Natural Resources to Lt. Colonel Howard N. Nicholas, District Engineer, Corps of Engineers. In setting forth these goals, it was recognized that extremes in weather variables in some years will preclude their precise attainment as described below. It was also recognized that annual reviews of the effectiveness of the regulations and problems involved would greatly facilitate the attainment of an optimum system of operations.

During severe flood and drought events the Corps of Engineers is impeded in regulating the Lake Winnebago Pool within the desired ranges of the ecological goals set forth above. During these events the capability to follow exactly the proposed procedures of regulation cannot be fully implemented and some latitude of operation will be required. For example, the low and high lake levels for 1979 occurred on March 17th and 18th at 0.63 feet (Oshkosh gauge) and on April 13th, 15th and 16th at 3.88 feet (Oshkosh gauge) respectively, even though all of the gates and needles at Neenah and Menasha were completely opened by March 5th. It should be noted that the maximum drawdown elevation of 0.63 feet is essentially the drawdown proposed above.

As shown by the 1979 spring flood event which is typical of the historical pattern of spring occurrences, it is almost impossible to prevent the lake level from rising once spring runoff begins. During the fall, the majority of the water leaving the lake flows over the spillway; thus there is no control over the subsequent decreasing lake level.

Appendix B. Scientific Names of Pertinent Species

Species Mentioned in Text	Scientific Name
Cattail	*Typha* spp.
Stiff arrowhead	*Sagittaria rigida*
Wildrice	*Zizania aquatica*
Common reed	*Phragmites communis*
Spike rush	*Eleocharis* sp.
Hard-stemmed bulrush	*Scirpus acutus*
Round-stemmed bulrushes	*Scirpus acutus* and *S. validus*
River bulrush	*Scirpus fluviatilis*
Clasping-leaf pondweed	*Potamogeton richardsonii*
American pondweed	*Potamogeton nodosus*
Sago pondweed	*Potamogeton pectinatus*
Canadian waterweed	*Elodea canadensis*
Wildcelery	*Vallisneria americana*
Water stargrass	*Heteranthera dubia*
Coontail	*Ceratophyllum demersum*
Water milfoil	*Myriophyllum* sp.
Lepidoptera	*Schoenobius* sp. and *Occidentalis* sp.
Common carp	*Cyprinus carpio*
Freshwater drum	*Aplodinotus grunniens*
Canvasback	*Aythya valisineria*
Forster's tern	*Sterna forsteri*
Muskrat	*Ondatra zibethica*

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Approximate English-Metric Equivalents

1 acre = 0.405 ha
1 ft = 0.305 m
1 inch = 2.540 cm
1 mile = 1.609 km
1 yd^2 = 0.836 m^2
1 qt = 0.946 L
1 oz = 28.035 g
1 lb = 453.592 g
1 ton = 0.907 metric ton

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About the Author

Rich Kahl is a wetland ecologist with the Wildlife Research Section of the DNR Bureau of Research and has been a wildlife research biologist with the bureau since 1985. His past and present research focuses on diving duck staging habitat and energetics, and on shallow lake management. His mailing address is Department of Natural Resources, Research Center, 1350 Femrite Dr., Monona, WI 53716.

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