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Editor

William J. Urbrock
College of Letters and Science
University of Wisconsin Oshkosh
Oshkosh, Wisconsin 54901

Managing Editor

Patricia Allen Duyfhuizen
328 West Grant Avenue
Eau Claire, Wisconsin 54701

Interns

Professor Wilma Clarke
Jan Kippenhan
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This paper presents a critical appreciation of the work of Wisconsin poet Ron Wallace, especially as represented in his latest book, *The Makings of Happiness.* Taylor discusses this book both as a collection of individual poems and as a remarkable narrative about mid-life progress.

From the editor

On this beautiful May morning, awash (after many rains!) in spring flowers and the first blossoms of fruit trees, several stray visitors have found their way into my office through an open window. I opened the window because the University's air conditioning has not been turned on for the season. The fresh air, of course, is the welcomed visitor. The most obvious unwelcomed guest is the sound of passing traffic on Algoma Boulevard, but my sneezes and itchy eyes remind me that pollen from the tulip beds beneath my windows has entered the office, too.

By far the most interesting visitor, however, is a magnificent queen bumblebee who has been trying for over two hours, without success, to find her way back to the window by which she entered! She has expended a good deal of energy attacking a closed window and the fluorescent lighting fixtures and now sits barely four feet away from me next to a heap of books, resigned, evidently, to a temporary life of scholarly contemplation. Since the books are piled right next to my telephone, it remains to be seen whether I will dare to answer if it rings!

By the time this 1993 issue of *Transactions* appears, circumstances in my office will have changed dramatically, I expect. Windows will be locked shut against the fall or early winter cold, the heating plant will be in action, pollen will have been replaced by late molds, pumpkins and squashes will represent the last hurrahs of the growing season, and according to my entomologist colleague down the hall, the queen bee may have settled into an abandoned mouse or bird's nest for overwintering—if she ever finds her way out of the office!

I have found my first year as editor of *Transactions* not unlike the experience just described. Saying "Yes" to the editorship has opened a window to visits by all sorts of new experiences, expected and unexpected, but almost all of them welcomed. Best among these has been the opportunity to make the acquaintance of and to collaborate with the outstanding array of authors, reviewers, and production staff represented by this issue.

I have been extremely impressed, for example, by the willingness of professional colleagues to spend much time, care, and energy on their review of manuscripts. I have enjoyed telephone conversations with many of them as well as the usual written correspondence. Some are my own colleagues at UW Oshkosh, whose expertise at reviewing I have only just discovered. As we all know, the work of reviewers often goes unheralded, although it is a scholarly service absolutely essential for ensuring that only articles worthy of publication and of further scholarly citation are actually published. Without fear of contradiction, I can speak for all the authors by acknowledging the debt they owe to the constructive criticisms and suggestions forwarded by their reviewers. All of us as readers are indebted as well to these reviewers, whose only compensation for their scholarly contribution is our "Thank You" and their own satisfaction at having furthered the cause of responsible research and of clear, accurate and reader-friendly written communication.

Of course, I also opened my window to the authors themselves, several of whom I have had the great pleasure of meeting on campuses and at workshops and conferences around Wisconsin during the past year. Altogether, the variety of research they report in this issue should be of interest to a wide spectrum of readers and should contribute to the related studies and research of many. And for all of us who simply take delight in learning more about the natural and human history of Wisconsin, there is much here to please: from a discussion of paleozoic landforms in the Baraboo Hills to an appreciation of John Muir's picturesque creation of the California Alps; from endangered cricket frogs in southwest Wisconsin, calcareous fens in the southeast, and parasitic fauna in eastern Elkhart Lake to deer mice and wild turkeys in the north and northwest; from paddlefish in the lower Wisconsin River to American brook lamprey in Taylor and Jambo creeks; from the red alga *Lemanea* in the streams of Marinette and Iron counties to the macrophyte community on Lake Mendota and to the summer phytoplankton on 579 Wisconsin lakes; from a history of early twentieth-century work in plant ecology in Wisconsin and the Midwest to a critical appreciation of a late twentieth-century midlife progress as portrayed by one of Wisconsin's premier poets.

Readers may notice an updated look in the design and layout of the 1993 *Transactions*, thanks to the artistic eye of our indefatigable Managing Editor, Patricia Duyfhuizen. Her contributions to the actual production of this journal are too many to begin to enumerate. Suffice it for me to express my gratitude to Tricia for transforming a heap of individual manuscripts into a finished publication of which members and supporters of the Wisconsin Academy justifiably may be proud. Thanks also to former editor Carl Haywood, *Wisconsin Academy Review* editor Faith Miracle, Executive Director LeRoy Lee, and my special on-site all-around advisor and collaborator at UW Oshkosh, Neil Harriman, for their generous assistance in helping me handle all the "visitors," expected and unexpected, who have come in through the window during this first year of my editorship.

Bill Urbrock

P.S. I trapped the queen bee in a cup and released her outside!

Omar M. Amin, Colleen A. Dickey, and
Alan R. Spallato

The impact of chemical rehabilitation on the parasitic fauna of fish in a Wisconsin lake

Abstract *A 23-ha, meso-eutrophic lake in eastern Wisconsin was treated with rotenone (1.5 ppm) in November, 1981, to kill its rough fish and restock with desirable fish populations. Pre- and post-treatment samples of fish were examined for parasites in September, 1981 and 1988, respectively. Moderately heavy infections with* Proteocephalus ambloplitis *(Cestoda) disappeared after the rotenone treatment, which killed its fish hosts, largemouth bass,* Micropterus salmoides, *and sunfish in 1981. Infections with* Neoechinorhynchus cylindratus *and* Leptorhynchoides thecatus *(Acanthocephala) decreased and increased dramatically, respectively, as a result of changes in their fish host populations following rotenone use. Metacercariae of* Posthodiplostomum minimum *(Trematoda) in sunfish and* Hysterothylacium brachyurum *(Nematoda) in largemouth bass were also present before and after the chemical treatment, respectively. The observed loss of* P. ambloplitis *after 1981 points to a possible method for its control.*

Efforts to establish desirable fish populations by rotenone treatment of lakes dominated by winter-kill resistant species, e.g., bullhead, and restocking have recently been attempted by the Wisconsin Department of Natural Resources, as well as by other agencies throughout the United States since the mid-1930s (Gilderhus et al. 1986). The impact of such chemical treatments on invertebrate and fish populations and consequently on their parasite fauna is, however, not known. The case of the recent chemical rehabilitation of Little Elkhart Lake in eastern Wisconsin provided an opportunity to examine the effect of chemically induced host population changes on the composition and prevalence of parasite species. Findings not only reflected answers to scientific curiosity, but also indicated a possible new approach to the control of some injurious fish parasites.

Materials and Background

Little Elkhart Lake is a 23-ha glacial lake that is 3 and 8 meters in average and maximum depth and 1.3 years in average water residence time, in Sheboygan County, eastern Wisconsin. The meso-eutrophic lake is an extension of hard ground water table with moderate nutrient level, e.g., total phosphorus, nitrogen, and alkalinity averaged 0.04, 1.0, and 124 mg/l, respectively, at various water depths. Dominant species of rooted aquatic vegetation included *Myriophyllum spicatum, Najas flexilis, Potamogeton illinoensis,* and *P. amplifolious.* Algae were present in low densities.

Before the chemical treatment in 1981, the fish population was dominated by black bullhead, *Ictalurus melas,* with a small number of northern pike, *Esox lucius;* walleye, *Stizostedion vitreum;* largemouth bass, *Micropterus salmoides*; bluegill, *Lepomis macrochirus;* pumpkinseed, *L. gibbosus*; black crappie, *Pomoxis nigromaculatus,* yellow perch, *Perca flavescens;* white sucker, *Catostomus commersoni*; golden shiner, *Notemigonus crysoleucas*; and yellow bullhead, *I. natalis.* A typical complex of lake invertebrates included abundant copepods and cladocerans and rare daphnias. Shore terrestrial vertebrates that may be involved in the life cycle of helminths infesting fish as larvae included many bird species (mallard, blue-wing, teal, wood duck, etc.) and mammals (mink, weasel, muskrat, raccoon, etc.); see Claggett (1981) for more details.

Little Elkhart Lake has a history of stunted sunfish and intermittent good largemouth bass populations. It is characterized by infrequent winter kill (1952, 1959), a chemical treatment and restocking with northern pike, largemouth bass, walleye, yellow perch, and golden shiner in 1961 (Schulz 1964, 1965), and subsequent accidental introduction of black bullhead, pumpkinseed, and largemouth bass by 1971. Black bullhead population increased as another winter kill in 1975 (Belonger 1976) caused weeds and undesirable fish species to become overabundant.

The lake was electroshocked to sample pre-treatment fish on September 22 and 23, 1981. On November 17, 1981, 220 gallons of rotenone were applied at a concentration of 1.5 ppm. Except for bullhead, total kill of all other fish species, including largemouth bass and sunfish, was noted. The crustacean and other invertebrate communities, however, remained practically intact (Nelson 1985a and pers. comm.). In May and June, 1982, the lake was stocked with 10,000 fingerling largemouth bass from Crystal and Gerber lakes, and 54,310 fingerling hybrid sunfish (bluegill x green sunfish) and bluegill from Beechwood Lake, as well as with 118 big largemouth bass up to 37 cm long. Subsequent electroshocking efforts in 1983 and 1984 demonstrated good survival of largemouth bass, sunfish hybrid, bluegill, and black bullhead (Nelson 1985b).

On September 1, 1988, a post-treatment sample of fish was similarly taken from the lake. Both pre- and post-treatment fish samples were promptly examined for parasites after transfer to the lab on ice. Parasites were systematically recovered and routinely processed for microscopical examination.

Results

Two fish species were collected and examined during each of the 1981 and 1988 surveys: largemouth bass (40 fish, 16–41 (mean 26) cm long in 1981 and 42, 17–28 (24) cm long in 1988) and bluegill (9, 13–18 (15) cm long in 1981 and 12, 10–20 (15) cm long in 1988). Largemouth bass and bluegill, along with all other species, except black bullhead, were totally eliminated from the lake as a result of the 1981 treatment. The 1988 samples were from new fish introductions mostly during 1982. Four pumpkinseed, 12 black crappie, and 13 yellow perch were also examined in 1981, and 7 black bullhead were examined in 1988.

In the 1981 pre-treatment study, the prevalence and intensity of *Proteocephalus ambloplitis* (Leidy) (Cestoda) infections in largemouth bass were moderate to heavy in intestinal and body cavity (gut surface, liver, spleen) locations (Table 1); only 27 mature gravid adults were localized in the intestine. The distribution of *P. ambloplitis* also extended into the body cavity of other fish species, e.g., 14 worms in 4 of 9 bluegill (Table 1), 1 in 1 of 12 black crappie, 6 in 5 of 13 yellow perch, and 4 in 2 of 4 pumpkinseed. In the 1988 post-treatment study, *P. ambloplitis* was absent from all sites in the 3 fish species examined then, including 42 largemouth bass, its major host.

The prevalence and intensity of *Neoechinorhynchus cylindratus* (Van Cleave) Van Cleave (Acanthocephala) was relatively high in largemouth bass before the chemical treatment but decreased by 1988. The opposite trend was observed in the other acanthocephalan *Leptorhynchoides thecatus* (Linton) Kostylev; its intensity of infection increased from 2.12 to 64.24 per examined fish in gut locations and from 0.37 to 0.93 in the body cavity of largemouth bass. Bluegill were not infected with either acanthocephalan species in 1981 but were considerably more frequently and heavily infected with *L. thecatus* than with *N. cylindratus* in 1988 (Table 1). In addition, 176 *L. thecatus* were also recovered from the gut of 5 of 7 black bullhead (48 worms) and the body cavity of 2 other bullheads (128) in 1988 .

In 1981, the sex ratio of *N. cylindratus* in largemouth bass was 1 male : 2.31 females (91% had eggs) and 1:1.44 in *L. thecatus* (all females had eggs). In 1988, the sex ratio was 1:0.61 and 1:0.63, in the same order. Gravid females of both acanthocephalan species were considerably less frequent than in 1981.

In addition, 33 *Posthodiplostomum minimum* (MacCallum) (Trematoda) were recovered from the body cavity of 3 of 4 pumpkinseed (32 metacercariae) and from the body cavity of 1 of 9 bluegill (1) in 1981, and 11 *Hysterothylacium brachyurum* (Ward and Magath) (Nematoda) were recovered from the body cavity (6) and intestine (5) of 7 of 42 largemouth bass in 1988.

Discussion

Parasite community succession stabilization was estimated to take at least 5 years from the initiation of major ecological shifts, e.g., impoundment (Becker et al. 1978). In this study, 8 years elapsed between the pre- and the post-treatment studies. Brown and Ball (1943), Sharma (1949), and Wright (1957) indicated that populations of microcrustaceans, e.g., *Daphnia* and *Cyclops*, were variably affected but not eliminated after treatment with rotenone. Major ecological shifts were shown not to deplete crustacean populations, e.g., copepods (Becker et al. 1978). The half life of rotenone in warm (24°C) and cold water (0°C) ponds in Wisconsin during September and March was 13.9 and 83.9 hr, respectively (Gilderhus et al. 1986). Rotenone at a concentration of 1 ppm remained toxic to bluegills in wire cages for 7–18 days in ponds during an Alabama winter but caused no residual deleterious effects upon subsequent bluegill production (Wright 1957). Mortality of caged fathead minnows, *Pimephalus promelas,* was 100% 48 hours after 0.15 mg/l rotenone treatment of a Wisconsin pond during September but

Table 1. Pre- and post-treatment surveys of parasites of *Micropterus salmoides* and *Lepomis macrochirus* in Little Elkhart Lake

			Pre-treatment (1981)		*Post-treatment (1988)*	
Fish species	*Parasite species*	*Site of infection*	*No. fish inf./ exam. (%)*	*No. of parasites (mean/exam. fish)*	*No fish inf./ exam. (%)*	*No. of parasites (mean/exam. fish)*
Micropterus salmoides	*Proteocephalus ambloplitis*	Intestine	34/40 (85)	138 (3.45)	0/42	0
		Body cavity	32/40 (80)	357 (8.93)	0/42	0
	Neoechinorhynchus cylindratus	Intestine	34/40 (85)	382 (9.55)	29/42 (69)	79 (1.88)
		Body cavity	2/40 (5)	2 (0.05)	0/42	0
	Leptorhynchoides thecatus	Intestine	10/40 (25)	85 (2.12)	41/42 (98)	2,698 (64.24)
		Body cavity	1/40 (2.5)	15 (0.37)	13/42 (31)	39 (0.93)
Lepomis macrochirus	*Proteocephalus ambloplitis*	Intestine	0/9	0	0/12	0
		Body cavity	4/9 (44)	14 (1.56)	0/12	0
	Neoechinorhynchus cylindratus	Intestine	0/9	0	1/12 (8)	1 (0.08)
		Body cavity	0/9	0	0/12	0
	Leptorhynchoides thecatus	Intestine	0/9	0	3/12 (25)	23 (1.92)
		Body cavity	0/9	0	6/12 (50)	28 (2.33)

declined to 0 after 72 hours (Gilderhus et al. 1986). These data support findings about the mortality of fishes and survival of Crustacea after the 1981 treatment of Little Elkhart Lake with rotenone.

The complete disappearance of *P. ambloplitis* from bass and sunfish is perhaps the most dramatic outcome of the 1981 chemical treatment. This clearly corresponded with the mortality of the definitive host, largemouth bass (where adult worms reproduce), and the principal intermediate hosts, e.g., bluegill and other sunfish species, and probably resulted from it, following the application of rotenone.

The mortality of sunfish in 1981 was also considered responsible for the dramatic decline in *N. cylindratus* population. The major intermediate host of this acanthocephalan species is bluegill (see Becker et al. 1978); other sunfish species are important paratenic (transport) hosts, e.g., pumpkinseed among others (Hoffman 1967). The fact that one of the paratenic hosts of *N. cylindratus* is black bullhead, which survived the 1981 chemical treatment, might have helped that acanthocephalan's marginal survival (Table 1).

The assumption that the loss of *P. ambloplitis* was related to changes in the fish and not the crustacean (cladoceran, copepod, or amphipod) host populations is based on the following. The increase in *L. thecatus* infections after the treatment must have been related to the survival of its amphipod intermediate hosts including *Hyalella* sp., e.g., *H. knickerbockeri* which is also an intermediate host for *P. ambloplitis*. The mortality of the definitive and paratenic hosts of *L. thecatus*, particularly largemouth bass and sunfish in 1981, indicates that *L. thecatus* could have only survived the chemical treatment in the crustacean host. The survival of *N. cylindratus* was also possible because of the survival of its ostracod intermediate host, possibly *Cypria* sp.

The complete eradication of the bass tapeworm, *P. ambloplitis*, by eliminating its fish hosts in a closed system like Little Elkhart Lake under the above conditions points to a practical method for the control of this injurious worm. This goal can be accomplished at the same time the quality of the fish fauna is being upgraded.

The loss of the light *P. minimum* infections after the 1981 treatment might have been affected by the mortality of its centrarchid fish intermediate hosts. The new *H. brachyurum* infections in bass after 1981 were probably introduced from stocking sources. The significant changes in the sex ratio and reproductive state of the two acanthocephalan species are not fully understood.

Acknowledgments

This work could not have been done without the help and cooperation of James McNelly, Larry Claggett, and John Nelson, Wisconsin Department of Natural Resources.

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__Omar M. Amin__ is the Director of the Institute of Parasitic Diseases while in the United States. He was formerly a Professor of Parasitology at the University of Wisconsin since 1971. A major focus of his work is the parasitology of wildlife, particularly of fishes from Wisconsin, North America, and elsewhere in the world. He has an MS in Medical Entomology from Cairo University and a PhD in Parasitology from Arizona State University.

__Colleen A. Dickey__ contributed to the post-treatment study while studying at the University of Wisconsin where she received her BS in Biology in 1989. She currently holds a Masters of Education from National-Louis University and teaches at the Glenview District in Illinois.

__Alan R. Spallato__ contributed to the pre-treatment study while studying at the University of Wisconsin where he received his BS in Biology in 1983. He worked at the Madison Hazleton Laboratories before he became an Environmental Chemist at the State Laboratory of Hygiene, Madison, Wisconsin, in 1989.

John L. Blum

Lemanea *(Rhodophyceae)* *in Wisconsin*

Lemanea Bory is a relatively large and firm, attached freshwater red alga. Seen underwater, it might easily be mistaken for a small vascular plant. It grows most conspicuously in and around waterfalls, thus in some of the more scenic and recreational sites. In the northern states, it is generally represented by a species of the subgenus *Lemanea* (formerly *Sacheria* Sirodot). The other subgenus (*Paralemanea*) consists of algae which are more complex in structure. Species of subgenus *Paralemanea* are well represented in the southern states, the Pacific states, and are especially abundant in the Ohio Valley, but have never been reported in Wisconsin. The closest collection appears to be from the Greencastle, Indiana, area. Because species of subgenus *Paralemanea* tend to occur where certain types of limestone are abundant (Palmer 1933, 1940, 1941), rapids of streams in southeastern Wisconsin where limestone strata are exposed probably represent the best possible places for finding members of *Paralemanea* within the state.

The earliest known Wisconsin collection of *Lemanea* subg. *Lemanea* was made by L. S. Cheney in 1894 in the vicinity of Stevens Point (precise location not identified) (MIN).* J. B. Moyle found it in the Black River (Douglas County) in 1940 (MIN), and J. W. Thomson also collected it there in 1942 (PH). The relative paucity of sites compared with other states led to a search for other possible locales. The author has more recently added other sites in the Pike (Dave's Falls), Pemebonwon (Long Slide Falls), and Peshtigo (Strong Falls) rivers (Marinette County), in the Potato (at Upson) and Montreal

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*Herbarium specimens referenced are in the Field Museum (F), the University of Minnesota Herbarium (MIN), and the Academy of Natural Sciences of Philadelphia (PH).

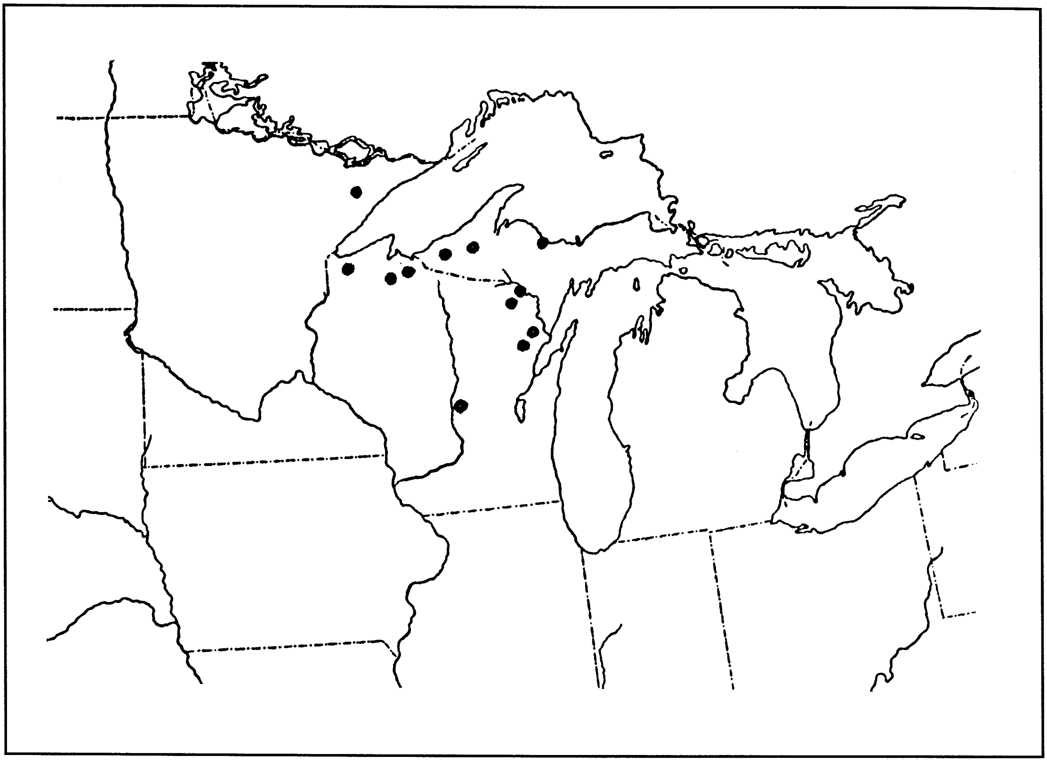


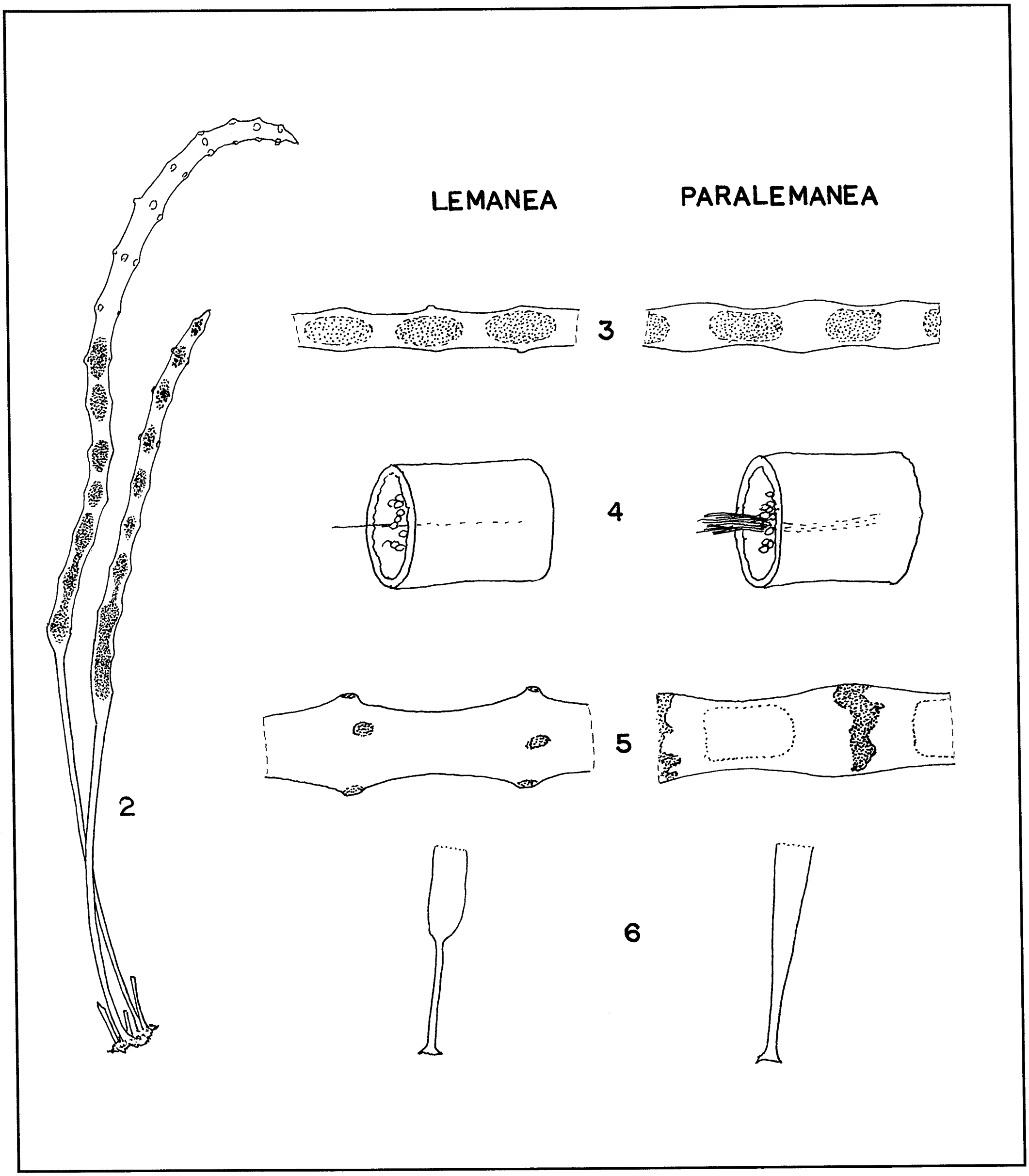
Fig. 1. Distribution of *Lemanea* (subgenus *Lemanea*) in the upper Great Lakes Region.

(near Hurley) rivers (Iron County), as well as sites in northern Michigan (Fig. 1), including Jackson Creek (Gogebic County) and the Ontonagon River (Ontonagon County). Vouchers will be deposited in F and elsewhere.

Lemanea appears to be abundant mostly over short reaches of streams. It reproduces sexually and produces large numbers of carpospores within the gametophyte thallus. Stewart (1983) and Sheath (1984) indicate that it can also grow as a perennial from attached basal filaments, and the author has found it growing at numerous sites in Indiana where C. M. Palmer found it forty or more years before.

Vis and Sheath (1992) have recently discussed and revised the taxa of *Lemanea* in North America. Their treatment permits identification of Wisconsin and Upper Peninsula material under the names of European entities, e.g., *Lemanea fluviatilis* (L.) C. Agardh and *L. fucina* Bory. In view of some uncertainties in the applications of these names, which I am unable to resolve, it seems preferable not to attempt the identification to species of my materials at this time.

The gametophytic plant of *Lemanea* bears, following fertilization, the carpospores. Various characters of the gametophyte thallus constitute the principal basis for differentiation of the two subgenera. This differentiation can usually be made with a hand lens. The thallus is nodose-cylindric in both subgenera with the carpospores visibly borne *en masse* internally at the "nodes" in subgenus *Lemanea* and at the internodes in subgenus *Paralemanea* (Figs.



Figs. 2–6. *Lemanea* (subgenus *Lemanea*) spore-producing plants from Long Slide Falls, Pemebonwon River, Marinette County, Wisconsin, collected 26 August 1985, *J. Blum #4764*. X 10. Figs. 3–6 show points of differentiation between spore-bearing plants of subgenus *Lemanea* and subgenus *Paralemanea*. Fig. 3. diagram shows relative position of the spore masses in relation to the "nodes." Carpospore masses are shown by stippling. Fig. 4. diagram contrasts the presence (subgenus *Paralemanea* with the absence (subgenus *Lemanea*) of rhizoids surrounding the axial filament. Fig. 5. diagram contrasts the position of the spermatangial areas (stipples). Fig. 6. diagram contrasts the bases of plants.

2, 3). This difference is less visible in certain species and certain specimens than in others. Sectioning the thallus reveals a single central axial filament in subgenus *Lemanea* whereas in subgenus *Paralemanea* numerous internal rhizoidal filaments surround the axial filament and constitute a strong central strand (Fig. 4) reminiscent of the stele in dicot roots. Observation of the central strand cannot easily be done with a hand lens, but free-hand sections reveal the essential point of distinction.

A third point of distinction is noted in the spermatangial (male) areas of the thallus, which are external and found at the nodes: subgenus *Lemanea* has protuberant spots of spermatogenous tissue whereas in subgenus *Paralemanea* the spermatangial areas form a nearly complete ring or band encircling the nodal areas (Fig. 5). Thus in subgenus *Lemanea* the gametangia of both sexes are found in the nodal areas; in subgenus *Paralemanea* they essentially alternate, with the nodes bearing the male gametangia and the internodes bearing the female gametangia. In early stages of growth, the minute trichogynes, the receptive external female structures, can be seen at 440X magnification. These trichogynes mark the areas where the (internal) future carpospore masses will develop; they appear on the flanks of the enlarged "nodes" in subgenus *Lemanea* and in the internodes in subgenus *Paralemanea.* The trichogynes can be seen in edge view on the silhouette of a thallus whole mount, as well as in surface view of a sufficiently cleared and stained specimen.

Lemanea carpospores are frequently ripe in populations of the eastern United States after approximately 1 July, and are dispersed when the thallus decays or breaks apart.

The fourth point of distinction is a simpler but less dependable one: the base of the gametophytic thallus in subgenus *Paralemanea* is regularly and gradually narrowed to its point of attachment, whereas in subgenus *Lemanea,* at least in Wisconsin material, there is frequently a distinct and non-nodose stipe (Figs. 2, 6) which is sharply marked off from an enlarged fertile upper part. Branching of the spore-bearing thallus in subgenus *Lemanea* is also more frequent than in subgenus *Paralemanea* or at least in the American species of *Paralemanea.*

All points of distinction can be misread: (1) The single axial filament in subgenus *Lemanea* is nearly approximated in some California *Paralemanea* species which may have only 2–4 internal rhizoids accompanying the axial filament. (2) The protuberant male areas in subgenus *Lemanea* are occasionally confluent within the nodal area and approximate the interrupted male "bands" in some material of subgenus *Paralemanea.* Additionally, this essential distinction is not easy to make without prepared slides and good microscope equipment. (3) The presence of carpospores in either nodal or internodal areas is a seasonal phenomenon and will not be observed in early spring or if fertilization has not occurred. The position of the female apparatus and carpospore masses is also considered a species character in subgenus *Paralemanea,* and in both subgenera, spores may escape from their usual position so that individuals are commonly seen with carpospores thoroughly scattered in the cavities of the gametophyte thallus. (4) The contrast between the gradually and the abruptly narrowed basal segment is frequently not pronounced.

The spore-producing haploid thallus alternates in its life history with a minute, filamentous stage, the *"Chantransia"* stage (Sirodot 1872; Atkinson 1890), which is a diploid plant. Meiosis occurs in apical cells of tiny branches that grow from the diploid, *Chantransia* stage (Magne 1967). The resulting haploid cells then develop into the macroscopic monoecious gametophytes; hence, the gametophytes develop from and are attached to the *Chantransia*. The *Chantransia* stage should not be disregarded by the collector. Bourrelly (1970) considers that the *Chantransia* stage is probably necessary for species determination in this genus. Summer collections of the spore-bearing thallus unfortunately are unlikely to have the *Chantransia* stage attached; after about 30 April, only fragments of it remain.

Summary

1. *Lemanea* (Rhodophyceae), erstwhile considered to be rare in Wisconsin, is shown to occur in streams of Iron and Marinette counties.

2. *Lemanea* may have permanent sites of residence in streams, since several places where it was collected over the past century have been successfully re-collected by the author in the 1980s.

3. Points of distinction between the two subgenera of *Lemanea* are summarized. Useful caveats in applying them are recommended and explained.

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***John L. Blum,** B.S., M.S., Wisconsin, Ph.D. Michigan 1953. Assistant Professor Biology, Canisius College, 1946–1963. Associate Professor and Professor of Botony, University of Wisconsin-Milwaukee 1963–1985. Associate Dean in Letters and Sciences (Science), UW-Milwaukee 1967–1969. Emeritus, 1985–date.*

Joshua C. Blumenfeld

Plant ecology comes of age in the United States

> Who were the first [ecologists] in America? Pound and Clements, Cowles, Gleason, Harshberger, and Harper, in about that order, followed very closely by Transeau and Shantz—
>
> Henry A. Gleason, 1953

The final years of the nineteenth century and the first half of the twentieth century saw not only the establishment of plant ecology as a discrete field of study, but the American dominance in vegetation theory and research (Tobey 1981). The later Wisconsin work of Curtis, McIntosh, and Cottam was built on the groundwork laid by this early, and predominantly Midwestern, group of ecologists. By the time Ernst Haeckel's term "oekologie" was officially changed to "ecology" by the Madison Botanical Congress of 1893, university programs in plant ecology were already well established, with the first ecological doctorate awarded in 1879 (Arthur 1895; Gleason 1953).

Two distinct schools of thought developed in America, both centered in the Midwest: one, a holistic/organismic tradition influenced primarily by Oscar Drude and the works of Alexander von Humboldt and August Grisebach, the other, a reductionist/individualistic tradition influenced by Johannes Warming and Augustin Pyramus de Candolle (Cowles 1898; Crawley 1986; Gleason 1953). The center of the holistic/organismic school developed at the University of Nebraska (chartered in 1869), while believers in the reductionist/individualistic school gravitated to the University of Chicago (founded in 1891) (Kormondy 1965; McIntosh 1976, 1985).

Tobey (1981) points out that one possible reason for Chicago's orientation was the university's policy of strictly pure research, as opposed to the land-grant college orientation of practical science:

> Chicago's ecology was concerned less with controlling than with preserving the natural world. [Nebraskan] ecology grew out of and returned for nourishment to the practical soil of agriculture.

John Merle Coulter, a former student of Asa Gray and, most recently, president of both Indiana University and Lake Forest College, arrived at the University of Chicago in 1891 (Rodgers 1944; Sears 1969). Coulter was but one member of an impressive faculty assembled to teach at the new university and was given the task of establishing the school's Department of Botany (McIntosh 1976).

Coulter was profoundly influenced by Warming's works and based a series of initial graduate lectures on them, hampered by the fact that, at the time, Warming's works were available only in the original Danish. However, as Charles Chamberlain, a graduate student in the class, recalled, "None of us could read Danish except a Danish student, who would translate a couple of chapters, and the next day Coulter would give a wonderful lecture on Ecology" (Chamberlain 1940).

One student in the lecture series grew impatient with this slow translating process and over time taught himself Danish, eventually reading Warming's works long before an English translation was available (Chamberlain 1940). This student was Henry Chandler Cowles (1869–1939), who would eventually become chairman of the department founded by Coulter.

Cowles received a fellowship to study geology at the University of Chicago in 1895, where he initially concentrated on landforms and plant fossils and was introduced to the glacial features and beach ridges of the Chicago area (Humphrey 1961). In addition, through Coulter's lectures, Cowles quickly grasped the new ideas put forth by Warming (Chamberlain 1940).

Coulter encouraged Cowles's interest in plant ecology, suggesting that Cowles combine his extensive knowledge of geomorphology with plant ecology to see if Warming's studies of Danish sand dunes was applicable to the dunes along Lake Michigan (Cook 1980). Cowles eventually turned the results of his findings into his Ph.D. dissertation, *An Ecological Study of the Sand Dune Flora of Northern Indiana* (1898).

By this time, Cowles was the recognized expert on plant ecology at the university, and Coulter called on him to teach most of the ecology courses. Aside from his teaching duties, Cowles took an active role in writing for the *Botanical Gazette*, founded by Coulter in 1875 and published by Coulter at the university. The *Gazette* was an ideal forum for the dissemination of Cowles's research, which was published in the journal between February and May, 1899 (Cowles 1899).

Through these papers, as well as two others published between 1899 and 1901, Cowles not only established himself as one of the pre-eminent plant ecologists of the time, but also formulated two concepts which, according to Cook (1980), form the center of his theories of vegetation:

> The paramount influence of the shape of the land—the topography—on the composition of plant communities, and the patterns of change over time by which one plant community succeeds another, leading gradually to a climax formation.

In his studies of the dunes of Lake Michigan, Cowles noted several distinct communities which replaced each other before terminating in a "mesophytic beech-maple deciduous forest," which Cowles interpreted as being the final community type (Cowles 1899). Cowles noted that each successive community altered the conditions of the dune, transforming what was originally a dry environment into a much more mesic environment (Cowles 1899).

In 1901, Cowles applied Warming's methods to the much broader area of "The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification of plant societies." Published in the *Botanical Gazette* and called "a landmark in the developmental study of vegetation" (Clements 1916), the article set forth Cowles's "physiographic theory" of vegetation. This held that, along with moisture content of the soil, topographic differences were necessary to permit a variety of plants to grow at similar moisture levels (Cowles 1901).

Cowles classified the landforms of Chicago and vicinity into different series and proceeded to describe the general succession pattern in each (Cook 1980; Cowles 1901). Cowles considered different plant species occurring on different landforms with an identical degree of soil moisture to be remnants of previous successive stages in the community development (Cowles 1901). Stressing that the past history of a landform had to be considered in any study of vegetation, Cowles stated that "the laws that govern changes in plant societies are mainly physiographic; whether we have broad flood plains, xerophytic hills, or undrained swamps depends on the past and present of the ever-changing topography. The idea of constant change must be strongly emphasized" (Cowles 1901).

After 1901, Cowles dedicated most of his time to teaching, earning a full professorship in 1915 and becoming chairman of the Department of Botany in 1925 (Humphrey 1961). As Gleason (1953) states, "[Cowles's students] were Cowles's chief contribution to ecology. Go through his printed works and you will soon see that his only important scientific contributions were in his few papers on succession."

While Coulter and Cowles were shaping plant ecology in Chicago at the turn of the century, Charles Edwin Bessey (1845–1915) was applying his ideas and experience in developing the botany program at the University of Nebraska.

Bessey began his studies in civil engineering, but soon concentrated his efforts on botany (Humphrey 1961). Like his contemporary, Coulter, Bessey worked his way West, serving on the faculty of Iowa's College of Agriculture for fifteen years before being invited to the University of Nebraska to establish their Department of Botany (McIntosh 1976). Bessey, too, was a student of Asa Gray and received much of his advanced botanical training from Gray at Harvard (Rodgers 1944).

One of Bessey's key undertakings was the formation of the Botanical Seminar (Worster 1977). Originally a rather loose association of undergraduate students, the seminar became formalized by the early 1890s and was given the task of cataloguing all the native vegetation of the state before it fell to the plow (McIntosh 1985). This became the start of the Nebraska Survey, lauded by George Vasey in 1893 as "setting an example, which if followed by other States, will soon give us a complete botanical Survey of the Country" (Rodgers 1944).

The students in the seminar were an incredibly strong group, most of whom came to botany from other fields and who would, eventually, form the basis for one branch of ecological thought. This school of thought was characterized by a holistic/organismic view of vegetation, much in the tradition of Drude, and was influenced greatly by Nebraska's topography (or lack thereof) and the nature of the land-grant college (McIntosh 1985). As Worster (1977) points out, while Cowles and Gleason observed succession on the individual sand dunes of Lake Michigan, Pound and Clements concentrated on the whole of Nebraska.

Roscoe Pound (1870–1964) was one of Bessey's students in the seminar. He began his studies in law, took degrees in botany, and ended up as dean of the Harvard School of Law where he established a reputation as a legal scholar (Pound 1954; Sears 1969). Pound, along with J. G. Smith, started the Botanical Survey of Nebraska and the Flora of Nebraska, and Pound credits himself with the idea of a Phytogeography of Nebraska (Pound 1954). However, after 1901 and the publication of *The Phytogeography of Nebraska*, Pound was forced to devote all his time to law.

Another Bessey student was Frederick Edward Clements (1874–1945), called "the greatest individual creator of the modern science of vegetation" (Worster 1977) and "the outstanding ecologist of his time and generation" (Phillips 1954). Among his many accomplishments, Clements is credited with developing the classical theory of succession, a view which dominated plant ecology well into the twentieth century and which is still used in vegetation classification today (Barbour, et al. 1987; Braun 1958; Whittaker 1962).

Frederick Clements was born in Lincoln, Nebraska, just down the road from the new University of Nebraska. Clements entered the University of Nebraska, receiving his B.S. in 1894, his A.M. in 1896, and his Ph.D. in 1898 (his alma mater would later confer the honorary degree of LL.D. in 1940) (Clements 1960; Humphrey 1961).

Clements eventually rose to full Professor of Botany at Nebraska, but resigned to accept the position of Professor of Botany and Head of the Department of Botany at the University of Minnesota (1905), where he remained until 1917. From 1917 until his death in 1945, he was associated with the Carnegie Institution of Washington, D.C., where he concentrated his work on soil conservation and the ecology of the West (Barbour et al. 1987; Pool 1954).

Clements's first work in vegetation was as a student in Bessey's Botanical Seminar, to which he was the first undergraduate admitted in 1892 (Tobey 1981). At that time, Pound was one of the graduate leaders of the seminar and was attracted to Clements "by his zeal, ability and diligence," recommending him for admission and putting Clements to work on the flora of Nebraska (Pound 1954).

By 1896, Pound and Clements were working together on the fungi of Nebraska. At this time, Pound got the idea of a phytogeography of the state. The resulting work, *The Phytogeography of Nebraska*, was published in 1898, partly as Clements's Ph.D. dissertation, and gained recognition as an important new work in the field (Cowles 1898; McIntosh 1976). It is interesting to note that one of the main reviews of the book is by Cowles in *Botanical Gazette* (1898, vol. 25), who considers the work "the pioneer work of its kind in America." Cowles also brings up a subject that would be a sticking point between plant ecologists and Clements throughout his publications—his creation of new terms and words "in place of the simpler and more expressive English equivalents" (Cowles 1898).

The Phytogeography of Nebraska deals

with a study of plant formations (as opposed to the Warming concept of plant societies), which Pound and Clements describe as either primitive or recent (Pound and Clements 1898). The recent classification is further divided into origin by nascence (occurring only on bare areas) and origin by modification (occurring through changes in existing communities). However, formation by nascence *always* occurs after a plant formation is destroyed "through the agency of fires, floods, man, etc." (Clements 1916).

Of particular importance is the introduction of the quadrat method of vegetation analysis, which Pound and Clements use to determine the structure and development of vegetation (Clements 1916; Pound and Clements 1898). Basically, the quadrat method is a means for determining the composition of vegetation in a large area by looking at the vegetation of limited, and representative, smaller areas (Curtis 1959; Gleason 1920; Pound and Clements 1898).

While Pound left the seminar to pursue law, Clements continued his ecological research. *Plant Succession* (1916), Clements's eighth book, not only introduced the concept of classical succession, but became one of the most important works on plant ecology, establishing a variety of concepts and a plethora of new terms and phrases. The work is mainly a summation of Clements's earlier research into the ultimate end of plant development (called the "climax"), first treated in *The Development and Structure of Vegetation* (1904) and again in *Research Methods in Ecology* (1905).

Clements was very forthright as to the purpose of the book, stating in the introduction that "the earlier concept of the formation as a complex organism with a characteristic development and structure in harmony with a particular habitat is not only fully justified, but that it also represents the *only* complete and adequate view of vegetation" (Clements 1916) [emphasis added].

Succession in general is concerned with the process of vegetation change—the way in which populations of a particular species are gradually replaced by populations of other species over time, usually making the original site more fertile and mesic (Braun 1950; Curtis 1959). In the Clementsian view of succession, a series of different plant communities (called "seres") will occupy a given site in a set pattern based on the history of the site (Pyne 1982). Knowing the location of a particular site, it is possible, according to Clements, to predict the pattern of change from pioneer species to the ultimate "climax" community, which is controlled by climate and is self-replicating (Clements 1936; Kormondy 1965). This optimum community is regarded as being a mesic forest, although Clements makes provision for deserts and aquatic communities (Clements 1916).

The most important aspect of this process is Clements's view of the climax community as an organism (Clements 1905). This "super-organism" view is not new, and is seen in the writings of Plato (viz. *Timaeus*) as well as in the concept of the Balance of Nature. As Clements describes it:

> The unit of vegetation, the climax formation, is an organic entity. As an organism, the formation arises, grows, matures, and dies. . .The climax formation is the adult organism, the fully developed community, of which all initial and medial stages are but stages of development (Clements 1936).

Like all of Clements's earlier works, *Plant Succession* introduced a multitude of new terms and definitions. As Gleason (1953) states, "To Clements, an association was soon regarded as an organism, and he really meant organism. You know Clements's passion for terminology: if he had not meant an *organism*, he would have coined a different word." As mentioned earlier, this emphasis on new terminology would be a continuing theme in the criticism of Clements's work, noted by, among others, Cowles (1898), Tansley (1935), Egler (1951), Gleason (1953), Phillips (1954), and Whittaker (1962).

Clements continued to develop and refine his ideas of succession and the climax community, culminating with "Nature and structure of the climax," published in the *Journal of Ecology* (1936). In this encompassing article, Clements presents the crux of what is considered classical or Clementsian succession. This work was followed in 1939 by *Bio-Ecology*, co-authored with Victor Shelford, in which the concept of the "biotic community" comprising both plants and animals (the "biota") was advanced. As Worster (1977) points out, even at this late date, Clements was insistent that it was the vegetation which determined the animals in a community, not the animals which determined the vegetation. By its recognition of animals as well as plants in the community, *Bio-Ecology* was able to unite the two fields of animal ecology and plant ecology and foreshadowed the development of systems ecology in the latter half of the century.

Whittaker (1962) points out three aspects of the Clementsian system which drew criticism: the erection of a formal system of classification based on hypothetical dynamic relations, the unlikely character of some of the successional relations required of the climax theory, and the inappropriateness of the system to the interpretation of natural communities. Curtis, in his landmark work *The Vegetation of Wisconsin* (1959), criticizes in particular the delineation by Weaver and Clements (1938) of the "Lake Forest" climax community to cover the vegetation of the upper Great Lakes and St. Lawrence valley, commenting that this "is an indication of the pitfalls that may be met when attempts are made to place vegetation into a preconceived framework without supporting quantitative evidence."

The Clementsian view of succession was not the only theory being developed at this time, and alternative theories of vegetation development were brought forth (i.e. Braun-Blanquet 1913; Cooper 1926; Ramensky 1926). Of these, the most influential in the U.S. was the individualistic concept of vegetation development, which was used extensively in the work of Curtis and his students at the University of Wisconsin and most closely identified with the work of Henry A. Gleason (1882–1975) (Curtis 1959; Whittaker 1962).

Gleason was yet another Midwesterner, growing up in Illinois and attending the University of Illinois (B.S. 1901, M.A. 1904) and Columbia University (Ph.D. 1906). Gleason returned to the University of Illinois; however, in 1910 he left for the University of Michigan and in 1919 joined the New York Botanical Garden (McIntosh 1975).

Gleason grew up at the prairie-forest edge and as early as 1909 was aware that factors other than climate were influencing the transition of prairie into forest (McIntosh 1975, 1985). Further, he recognized that different types of communities could, and did, invade similar areas (Gleason 1909).

After the publication of *Plant Succession*, Gleason replied with an article entitled "The structure and development of the plant association" (1917). Gleason presents four main problems with Clements's arguments: (1) the view of the unit of vegetation as an organism, (2) the inclusion not only of the climax but of all stages leading to the climax as part of the vegetation unit, (3) a view of vegetation so complex that it requires the burdensome addition of many new terms, and (4) the exclusion of exceptions to Clements's views of plant community development "by definition" (Gleason 1917).

Gleason then proceeds to list twenty-eight points in sketching out what he calls the "individualistic concept of ecology." This thesis holds that "the phenomena of vegetation depend completely upon the phenomena of the individual [plant]" and that "individuals of the same species may occupy apparently different habitats and have different associates in different localities." Gleason points out that while many seeds of a particular species may enter an area through dispersal, the germination of a particular seed is dependent on the surrounding vegetation and the environment: those species which are best adapted to a particular combination of vegetation and environment will be selected. As Gleason states, "the association represents merely the coincidence of certain plant individuals and is not an organic entity of itself."

One important concept raised by Gleason in his article is the idea of transition zones between vegetation associations. These zones are areas of species mixing where one association ends and another begins, much like the tension zone presented by Curtis for the state of Wisconsin (Curtis 1959). This is in contrast to the Clementsian view, which holds that one would find no such mixing, but, rather, a more abrupt shift between communities as one climax turns into another (Curtis 1959; Gleason 1917; Whittaker 1962).

Finally, Gleason challenges Clements on the unidirectional trend of the climax, stating that while forest may succeed prairie, the opposite is also seen, termed retrogressive succession by Gleason. Clements denies the existence of these reversals and, according to Gleason, excludes them from his system through definition. Gleason formalized his individualistic concept in his landmark article "The individualistic concept of the plant association" (1926).

Gleason states that the two factors which most influence the structure of a plant association are the environment and the surrounding vegetation. While the vegetation of a particular area may show a great deal of homogeneity (such as the Wisconsin portion of the Mississippi Valley), this uniformity is lost when one takes a larger geographic view (such as the entire Mississippi Valley).

It is this diversity in space which forms the basis for the individualistic concept of the plant association: "The plant individual shows no physiological response to geographical location or to surrounding vegetation *per se*, but is limited to a particular complex of environmental conditions, which may be [affected] by the vegetation" (Gleason 1926). That is, a viable seed which migrates to an area of favorable environmental and vegetation conditions will germinate, while those falling into unfavorable conditions will not. To Gleason, chance, rather than a predetermined series, plays the crucial role in the appearance of the community.

To account for succession, Gleason presents a model where, because of changes in the environment, older species find it increasingly difficult to propagate. At the same time, seeds of outside species are constantly entering. Eventually the environment will pass the physiological limits of the old species and become favorable to the migrants, which proceed to propagate rapidly and thus change the form of the community. As Gleason states, "the next vegetation will depend entirely on the nature of the immigration which takes place in the particular period when environmental change reaches the critical stage" (Gleason 1926).

To say that Gleason's concepts generated criticism would be an understatement. As Gleason recounts, his concept was debated in 1926 at the International Botanical Congress and met with sharp disagreement and ridicule (Gleason 1953). By the end of the conference, the taxonomists still supported Gleason, but the ecologists would have no part of him, in effect ostracizing Gleason for about ten years (Gleason 1953).

As McIntosh (1975) points out, until the late 1940s, Gleason's concepts were essentially ignored in the popular texts of the period, appearing in only one textbook, *Plant Ecology* (McDougall 1927), and then barely mentioned. However, in 1947, F. E. Egler, S. A. Cain, and H. L. Mason all published articles in *Ecological Monographs* strongly supporting Gleason's individualistic concept of the plant association. It is interesting to note that this revival of the individualistic concept occurred only after the death of Clements in 1945.

By the time the articles came out, Gleason had stopped publishing articles on ecology (his last strictly ecological article appeared in 1939) and devoted his efforts to taxonomy, a field in which he excelled and found more support (Steere 1958). McIntosh (1975) notes that Gleason is probably the only person who is cited in bibliographies as both the author of a major ecological concept and the source of the plant nomenclature used.

The works of the European ecologists exerted great influence on the development on the Clementsian and Gleasonian theories and concepts. In fact, it appears that an individualistic concept of the plant association was put forth in a number of countries at about the same time: Ramensky in Russia, Negri in Italy, and Lenoble in France (Kormondy 1965; McIntosh 1975). Ramensky's ideas are remarkably similar to those of Gleason; he presents a concept of vegetation continuity and species individuality in his "Die grundgesetzmassigkeiten im aufbau der vegetationskecke," published in 1926, the same year as Gleason's article. Ramensky also states that observation of communities cannot be done by a reduction of the community to small units. Rather, he suggests the use of statistical surveys of greater areas and the averaging of these surveys, which would include such factors as frequency and abundance, a method which bears striking resemblance to that used by Curtis in *The Vegetation of Wisconsin* (1959) (Kormondy 1965).

The Clementsian school also had its European supporters, including Sukachev (or Sukatchew) in Russia, who likewise viewed the community as a distinct entity. It appears that the Ramensky/Sukachev difference was essentially a Russian version of the Gleason/Clements arguments, with Sukachev taking a dominant role and the works of Ramensky being suppressed for quite some time after publication (Kormondy 1965; McIntosh 1975).

Clements and Gleason were not the only ecologists in America making headway in plant ecology during the first half of the century. As Gleason points out, a number of ecologists contributed to the establishment of plant ecology (Gleason 1953). Two who made large contributions to plant ecology at the time are John W. Harshberger and William S. Cooper.

John W. Harshberger (1869–1929) spent his academic career in Philadelphia and concentrated his studies primarily on plant geography (Humphrey 1961). By far his greatest contribution to plant geography is the authorship of volume 13 of *Vegetation der Erde: Phytogeographic Survey of North Amer-*

ica (1911). While many considered this work unreliable and inaccurate, Egler (1951) points out that this work "presents an overall picture of what vegetation *is*, rather than what the successions and climax theoretically are."

Among Harshberger's more regional studies are "An ecological study of the New Jersey strand flora" (1900) and "An ecological study of the flora of mountainous North Carolina" (1903). Of particular interest in the "North Carolina" article is the recognition of shade tolerant and shade intolerant trees, which Harshberger proceeds to classify. Like Curtis (1959), Harshberger recognizes sugar maple as being the most shade tolerant while white oak is placed near the bottom of the tolerance list. Overall, Harshberger recognizes that the vegetation of an area becomes stratified due to changing conditions of moisture and light. Whittaker (1962) credits this article as being one of the first to distinguish the formation and the association in their modern senses.

William S. Cooper, a student of Cowles, directed his research at the University of Minnesota toward studying succession and the mechanisms behind the climax community (McIntosh 1985). While Cooper studied succession throughout the United States, his very detailed studies on Isle Royale are of particular note to the Midwest.

After studying trees and vegetation, Cooper reached the conclusion that a linear succession did not necessarily exist. Rather, vegetation was in the form of a "flickering mosaic" in a state of continuous change brought on by small disturbances, especially windfalls (Cooper 1913, McIntosh 1985).

Cooper's ideas of vegetation change are most succinctly stated in "The fundamentals of vegetative change" (Cooper 1926). Cooper emphatically rejects the Clementsian concept of the super-organism to represent the development of the plant community, stating that while the concept of an organism is convenient in the descriptive sense, its application to vegetation in a biotic sense is totally unwarranted.

To describe the development of the plant community, Cooper proposes a model of a braided stream. Cooper begins with two premises: (1) the universality of change, that is, a study of vegetation must include not only the present but also the past, and (2) the field of study must include *all* types of vegetation change. Cooper then likens the vegetation of the earth to a flowing stream, which is composed of braids and which has its headwaters in the distant past. While many small streams strive to take an individualistic path, the merging and simplification is balanced by a growing diversification in species. These changes may be fast or slow, with the so-called climax community representing a stream which is changing at an imperceptibly slow rate. As Cooper summarizes, "Vegetational change is due to the interaction of changing organisms and changing environment, just as the contour of a stream is continually modified by the interaction of its changing current and changing banks."

This, then, was the state of plant ecology at the end of the first quarter of the twentieth century. Establishment of the Ecological Society of America in 1915 did much to advance the spread of research in the field by bringing together both plant and animal ecologists, while the journals of the Society, *Ecology* and *Ecological Monographs*, served as the American outlets for ecological research (Sears 1969).

From its first formal beginnings at Chicago and Nebraska, plant ecology literally burst upon the scientific consciousness in the twentieth century, not only establishing itself as a formal and respected field of professional study, but supplying the initial paradigms of thought—the Clementsian and Gleasonian views of community development. Supplemented by the theories of Harshberger and Cooper, among others, plant ecology entered the next phase of its development in the United States. The University of Wisconsin played a key role in this next phase, with the works of Curtis, McIntosh, and Cottam helping to synthesize the Clementsian and Gleasonian views in the creation of a more modern view of community development aided by mathematical and statistical analysis.

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Joshua C. Blumenfeld received his M.S. in Land Resources from the Institute for Environmental Studies at the University of Wisconsin-Madison. His previous research has dealt with plant community ecology and the history of plant ecology in the United States.

Quentin J. Carpenter and Calvin B. DeWitt

The effects of ant mounds and animal trails on vegetation pattern in calcareous fens

Plant communities are not distributed randomly over the landscape, but are correlated with various climatic, topographic, geologic and biotic factors, including many anthropogenic features (Jenny 1980). Similarly, most plant communities are not homogenous, and the distribution of species within a community is correlated with special niches (Whittaker 1970). In calcareous fens, some previous authors (e.g., Frederick 1974; Reed 1985; Boyer and Wheeler 1989) have noted a two-part pattern in many (but not all) sites. This pattern consists of a zone of taller herbaceous vegetation, termed "Fen Meadow" (Frederick 1974), contrasted with a short zone, described as "Marl Meadow" (Fredrick 1974) or "Discharge Window" (Reed 1985). The "Marl Meadows" often include many of the "Fen Meadow" species in depauperate form, but they also include other uncommon or rare species, not found generally distributed on the fen. Recent studies suggest that this tall-short contrast may be due to geochemical processes which affect the availability of phosphate and potassium to the plants (Boyer and Wheeler 1989; Wassen et al. 1990).

In observing a number of fen communities in southern Wisconsin, we have noticed two other possible sources of vegetation heterogeneity, both of them biotic: ant mounds and mammal trails. Ant mounds, while not usually common on fens, are very noticeable, often rising 10 to 30 cm above the general surface and bristling with vegetation. A few ant mounds are a meter in diameter, but most tend to be less than 0.5 m across. Bruskewitz (1981) found that the locations of ant mounds were positively correlated with the occurence of shrubs on the Waubesa Peat Mound Fen in southern Wisconsin, but did not examine the relationships of other species to ant mounds. The species of ant which builds mounds on calcareous fens in this area is *Formica montana* [= *Formica cinerea montana*], the same species which is responsible for most mound building on Wisconsin prairies (Greg Henderson, pers. comm., 1988). Studies of this species at a wet prairie site in southwestern Wisconsin found that hydraulic conductivity and nutrient availability were higher in the ant mounds than in the surrounding gleyed soil; vegetation-ant relationships were not studied (Dening et al. 1977).

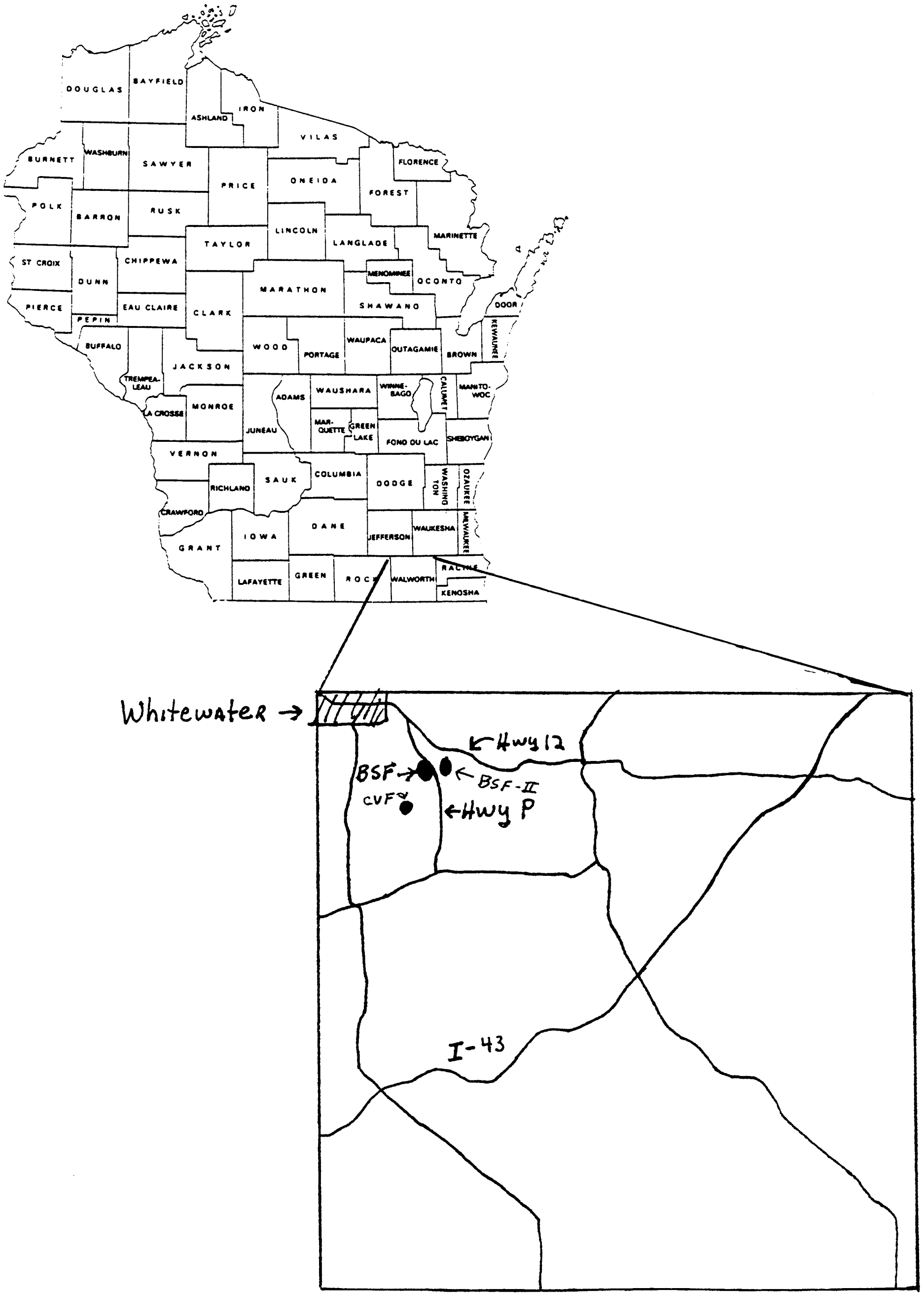
The mammal trails through the zone of tall vegetation ("Fen Meadow") appear to be made by deer, muskrats, raccoons, and humans. Our observations suggest that these trails often contain species which we more commonly find in the "Marl Meadows" zone; in fact, animal trails are often the only place where we noted these species in fens where no clear "Marl Meadow" zone was identifiable. The present study was designed to test our perceptions by obtaining quantitative vegetation data to answer the following two questions:

1. Is the vegetation found on or near fen ant mounds significantly different from that of the fen in general?
2. Is the vegetation found on or near trails made by animals across fens significantly different from that of the surrounding fen?

Methods

All ant mounds on three calcareous fens in Walworth County, Wisconsin, were marked while collecting general vegetation data from these sites for a related study (Carpenter 1990 and unpublished). Nine ant mounds were located on Bluff Springs Fen I (BSF-I), 18 on Bluff Springs Fen II (BSF-II), and 15 on Clover Valley Fen (CVF) (Fig. 1). During late summer or early fall, the vegetation on and immediately surrounding each of these ant mounds was surveyed using a square 1 m^2 quadrat frame centered on the ant mound, while the general vegetation of the fens was surveyed using the same apparatus randomly placed within cells of a grid system which covered most of each fen (Carpenter 1990). Species abundance data were recorded as per cent cover. After arc-sin square root transformation, means for each species found in quadrats centered on ant mounds on a particular fen were compared to means of the same species obtained from the general survey of the same fen using an unpaired t-test (Snedecor and Cochran 1980). Because the ant mound surveys and the general vegetation surveys were not conducted at the same time (time differences varied from two to four weeks depending on the site), a conservative standard of difference ($p < .01$) was adopted recognizing that the relative abundances of many species change gradually throughout the season.

To determine if the vegetation on or very near animal trails differed from the adjacent fen vegetation, 15 quadrat pairs were read on BSF-I on 16 September 1988 and 13 quadrat pairs on BSF-II on 30 September 1988; a distinct animal trail of sufficient length to provide at least 10 paired sampling locations could not be located on CVF. The 1 m^2 quadrat pairs shared an edge and were spaced at 5 m intervals along a fisherpersons' trail (BSF-I) and a deer trail (BSF-II) which crossed the respective fens east-west. At each sampling point, the quadrat frame was first read centered on the trail. It was then flipped over, to the south at the first sampling point, to the north at the second, etc., such that 15 (or 13) vegetation samples were obtained centered on the trail, and 15 (or 13) samples were obtained centered 1 m off the trail in



County.

Fig. 1. Location of study site in Wisconsin and Walworth County. Source: State Cartographers Office, Madison.

nearly equal numbers on either side of the trail. As in the ant mound survey, abundance data were collected as per cent cover, then arc-sin square root transformed for statistical analysis. Because of the small sample size, only those species which attained at least 0.5% mean cover were subjected to statistical analysis. Means were compared using a paired t-test (Snedecor and Cochran 1980). Since the paired design of this part of the study allowed better control of time and distance disparities, a less rigorous standard of difference ($p < 0.05$) was used.

Results

Table 1 summarizes the results of the general fen vegetation versus ant mound vegetation study. Only one species, *Muhlenbergia mexicana*, was found to be significantly more common (at $p < 0.01$) on or near ant mounds when all three fens were lumped. Three other grasses, *Andropogon gerardii, Bromus ciliatus* and *Sorgastrum nutans,* met a lower standard ($p < .05$) on at least two of the three fens, suggesting a possibly weaker association with the ant mounds. No broadleaf herb or shrub met either standard.

Tables 2 and 3 present summaries of the data from the mammal trail surveys for BSF-I and BSF-II. Thirty six taxa met the 0.5% mean cover criterion on at least one fen; fifteen of these taxa were shared by both fens. The data from Tables 2 and 3 suggest that 38% of the taxa considered from BSF-I and 44% of those considered from BSF-II were affected significantly ($p < 0.05$) by the proximity of trails. Nevertheless, while each fen contained many species affected by trails, only three taxa (*Lobelia kalmii, Parnassia glauca,* and bare ground) were significantly more common on trails in both fens; *Parnassia glauca* was strongly favored ($p < 0.01$) on both sites. Only detritus was negatively associated ($p < 0.05$) with trails on both fens. Disregarding significance, eleven of the fifteen taxa in common varied monotonically (i.e., the taxon increased or decreased on both fens), while four species did not. No taxon was significantly favored on one fen, but significantly disfavored on the other.

Discussion and Conclusions

Muhlenbergia mexicana and perhaps some of the prairie grasses are more common on and

Table 1. Summary of distribution of *Muhlenbergia mexicana* on three fens in Wisconsin. Mean cover on ant mounds was compared to that over the general fen using an unpaired t-test.

	Ant mounds		*General Fen*		*p-value*
Site	*mean % cover*	*presence*	*mean % cover*	*presence*	*(cover)*
BSF–I	23	8/9	0.15	2/20	p<0.001
BSF-II	12	10/18	1	7/30	p<0.01
CVF	10	8/15	1.5	13/29	p<0.03
Combined data	13.6	26/42	1.0	22/79	p<0.01

Table 2. Summary of trail study on Bluff Springs Fen I, 26 August 1988.

Species tested	*Raw mean on trail (% cover)*	*Raw mean off trail (% cover)*	*Raw difference (on-off)*	*t-value after arc-sin sqrt transform)*	*Significantly different @ 5% level*	*Significantly different @ 1% level*
Aster lateriflorus	*0.9*	*0.9*	*0.0*	*0.00*		
Aster puniceus	*1.8*	*1.3*	*0.5*	*1.76*		
Carex leptalea	*2.1*	*3.9*	*-1.9*	*-1.77*		
Circium muticum	*0.9*	*0.9*	*0.0*	*0.00*		
Cornus stolonifera	*1.1*	*11.1*	*-10.0*	*-3.16*	*D*	*D*
Eupatorium maculatum	*0.5*	*1.7*	*-1.2*	*-1.89*		
Eupatorium perfoliatum	*1.0*	*1.7*	*-0.7*	*-0.63*		
Gerardia purpurea	*0.6*	*0.2*	*0.4*	*2.52*	*F*	
Lobelia kalmii	*0.9*	*0.6*	*0.3*	*2.19*	*F*	
Lysimachia quadriflora	*2.0*	*1.1*	*0.9*	*2.10*		
Muhlenbergia glomerata	*1.7*	*2.6*	*-0.9*	*-1.12*		
Panicum flexile	*1.6*	*0.7*	*0.9*	*2.46*	*F*	
Parnassia glauca	*2.6*	*1.0*	*1.6*	*3.87*	*F*	*F*
Rhynchospora capillacea	*9.5*	*2.5*	*7.0*	*2.12*	*?*	
Rudbeckia hirta	*0.9*	*0.7*	*0.1*	*0.78*		
Scirpus acutus X validus	*3.3*	*3.9*	*-0.6*	*-0.32*		
Scleria verticillata	*14.0*	*4.5*	*9.5*	*3.56*	*F*	*F*
Solidago ohioensis	*6.7*	*6.9*	*-0.3*	*0.32*		
Sorgastrum nutans	*6.4*	*4.8*	*1.6*	*1.24*		
Bare ground	*10.0*	*1.9*	*8.1*	*5.41*	*F*	*F*
Dead material	*9.0*	*11.0*	*-2.0*	*-2.32*	*D*	

Data are from 15 paired 1-m-square quadrats centered either on or 1 m from the center of a human trail. After arc-sin square root transformation, differences in means were compared using a paired t-test. An "F" indicates a taxon significantly more common on or near a trail (= Favored). A "D" indicates a taxon significantly less common on or near the trail (= Disfavored).

around ant mounds than in the general fen. From observations of the behavior of the mound-building ant *Formica montana* on the Whitewater area fens over several seasons, we suggest the following explanation for this association: during April the ants clear away all dead material on or near their mound; during May and the early part of June, they prune any green shoots which erupt through the mound. During the summer, however, shoots are allowed to grow and often drape over the mound. We suspect the ants' vegetation management is related to thermo-regulation of the ant mound, removing shading vegetation in the cool spring, but allowing it to grow in the hot summer. Whatever the reason for the ant behavior, the repeated cutting of shoots seems to favor late-season grasses, which often do not emerge until June and which flower in the late summer. Further, we have observed that, of all the grasses found on fens, *Muhlenbergia mexicana* is the last to flower, sometimes as late as early October; we suspect that the strong association between this grass and the ant mounds is

Table 3. Summary of trail study on Bluff Springs Fen II, 16 September 1988.

Species tested	*Raw mean on trail (% cover)*	*Raw mean off trail (% cover)*	*Raw difference (on-off)*	*t-value (after arc-sin sqrt transform)*	*Significantly different @ 5% level*	*Significantly different @ 1% level*
Aster junciformes	0.2	0.6	-0.5	-2.82	D	
Aster lateriflorus	1.9	1.5	0.4	1.95		
Aster puniceus	1.0	1.1	-0.1	-0.13		
Betula pumila	14.2	21.9	-7.7	-1.72		
Carex lasiocarpa	2.3	2.3	0.0	-0.00		
Carex leptalea	9.4	4.4	5.0	3.69	F	F
Carex sterilis	7.7	6.1	1.6	1.38		
Carex stricta	8.2	9.8	-1.5	-0.53		
Cladium mariscoides	1.3	0.9	0.4	0.47		
Comandra richardsiana	1.4	0.2	1.2	2.33	F	
Cornus stolonifera	1.9	5.8	-3.8	-1.08		
Eleocharis rostellata	3.8	1.9	1.9	1.26		
Eupatorium maculatum	0.9	1.8	-0.9	-0.34		
Galium boreale	1.9	3.1	-1.2	-2.17		
Lobelia kalmii	1.1	0.2	0.9	5.55	F	F
Lysimachia quadriflora	1.3	0.7	0.6	3.09	F	F
Muhlenbergia glomerata	5.9	2.1	3.8	5.78	F	F
Muhlenbergia mexicana	1.2	0.7	0.5	0.21		
Parnassia glauca	1.2	0.3	0.9	3.73	F	F
Potentilla fruticosa	18.5	28.8	-10.4	-2.43	D	
Pycnanthemum virginianum	1.3	0.8	0.5	1.19		
Rudbeckia hirta	0.7	0.1	0.6	2.21	F	
Scirpus acutus	4.6	4.8	-0.2	-0.27		
Solidago gigantea	0.5	0.7	-0.2	-0.49		
Solidago ohioensis	5.3	1.8	3.5	4.96	F	F
Solidago uliginosa	1.6	0.2	1.4	4.69	F	F
Sorgastrum nutans	5.0	2.5	2.5	1.57		
Typha latifolia	1.3	1.2	0.2	-0.05		
Valeriana cilliata (edulis)	2.5	0.8	1.7	3.28	F	F
Viola cuculata	1.1	0.6	0.5	1.50		
Bare ground	5.3	2.6	2.7	2.78	F	
Detritus	8.5	17.5	-9.0	-2.90	D	

Data are from 13 paired 1-m-square quadrats centered either on or 1 m from the center of a deer trail. After arc-sin square root transformation, differences in means were compared using a paired t-test. An "F" indicates a taxon significantly more common on or near the trail (= Favored). A "D" indicates a taxon significantly less common on or near the trail (= Disfavored).

somehow related to this trait. The increased hydraulic conductivity and nutrient availability found by Denning et al. (1977) may also play a role in favoring grasses on or near ant mounds.

The trail at the base of BSF-I is used primarily by persons trout fishing in Bluff Creek and to a lesser extent by deer, raccoons, and mink, while the trail on BSF-II appears to be used mostly by deer. Most of the species favored by the trails, such as *Carex leptalea* and *Lobelia kalmii*, are also small, and were classified as "competition-intolerant species" by Zimmerman (1983). If this classification is correct, they would be expected to benefit from the trampling in the center of a trail which might more adversely affect some of the larger competitors. Others, however, such as *Solidago ohioensis* and *Muhlenbergia glomerata*, are among the tallest and most common herbs on these fens (Carpenter 1990); thus, the single explanation of competition intolerance may not apply to all species affected. We suggest that the increased vigor of the apparently more competitive species may be analogous to the pattern one sees along a sheep or cattle trail in a pasture where the grass grows tallest and greenest just at the edge of a trail (personal observation). The simplist explanation for this observation is that the taller and greener plants are far enough away from the center of the trail to avoid trampling, yet close enough to the trail to benefit from the extra nutrients found in manure and urine.

The disfavored shrubs (*Cornus stolonifera* on BSF-I and *Potentilla fruticosa* on BSF-II) may be victims of browsing or are perhaps simply killed by trampling when small. One might speculate that the trails were simply rerouted around shrubs; however, inspection of several aerial photos of the sites (1947 to 1980) suggests that the trails are long established and relatively straight.

The idea of trails, especially human trails, across natural areas is a complicated and often emotional issue. On the one hand, the evidence presented here suggests that trails provide special habitat for some uncommon competition-intolerant species; on the other hand, trails provide access for humans to damage the integrity of the natural area by excessive trampling, flower picking and inadvertant introduction of exotics such as purple loosestrife (*Lythrum salicaria*) and fen buckthorn (*Rhamnus frangula*). Many disturbance or pioneer wetland species are commonly associated with fens (Zimmerman 1983). Observations from fens in Wisconsin, Iowa, and Ohio (Zimmerman 1983; Loeschke 1991; Denny 1991) which have had their surfaces severely disturbed but have maintained their former groundwater supplies suggest that many of the rare competition-intolerant species such as *Scleria verticillata, Parnassia glauca,* and *Rhynchospora capillacea* appear in great abundance after disturbance. Thus, we suggest that all disturbance is not detrimental to fens and that managers must judge specific types of disturbances on their individual ecological merits or dangers.

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***Quentin Carpenter** is a dissertator in the Land Resources Program of the Institute for Environmental Studies, University of Wisconsin-Madison; his research concerns the interaction of hydrology and vegetation in calcareous fens of southern Wisconsin.*

***Calvin B. DeWitt** is Professor of Environmental Studies, Institute for Environmental Studies at the University of Wisconsin-Madison. His teaching and research concerns include wetland ecology, land use ethics, and stewardship of the earth.*

Lee Clayton and John W. Attig

Exhumed early Paleozoic landforms on the Baraboo Hills, Wisconsin

Abstract *The Baraboo Hills of southern Wisconsin consist of extremely durable Precambrian quartzite. Some of the well-preserved landforms seen there today were formed during the early part of the Paleozoic, were then buried, and were subsequently exhumed in Mesozoic or Cenozoic time. Valleys in the western part of the South Range were cut in Middle Cambrian time or earlier and buried in Late Cambrian time. Subsummit benches and scarps were cut by marine shore erosion in early Ordovician time and buried soon after. Summit plateaus were cut by subaerial or marine-shore processes, probably in Middle Ordovician time, and buried in Late Ordovician time.*

The Baraboo Hills of south-central Wisconsin (Fig. 1) contain some remarkably well-preserved Paleozoic landforms. Late Cenozoic landforms are present, but in this paper we conclude that many of the landforms were cut into the Baraboo quartzite early in the Paleozoic, buried soon thereafter, and exhumed in late Mesozoic or early Cenozoic times. These Paleozoic landforms include valleys, subsummit benches and scarps, and summit plateaus.

Although some of these landforms were recognized more than a century ago (Irving 1877, 504–05), they were poorly known until studied by Thwaites (1931, 1935, 1958, 1960). However, some elevations on the topographic maps available to Thwaites are in error by more than 100 m, and some features are misplaced horizontally by as much as 1 km. As a result, Thwaites was unable to adequately document the location and elevation of the landforms or to convincingly demonstrate the relationship between these landforms and the Paleozoic formations of the area.

Accurate topographic maps now exist, and the geology of the region has been mapped in greater detail (Dalziel and Dott 1970; Clayton and Attig 1990; Attig and Clayton 1990; Attig et al. 1990). As a result, we now are able to document the el-

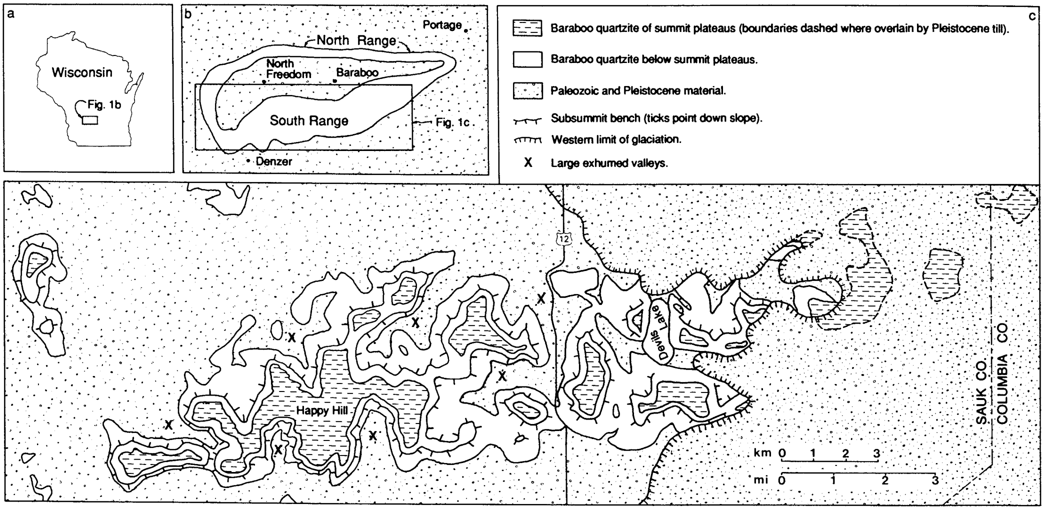

Fig. 1. Location of landforms of the South Range of the Baraboo Hills.

evation and the location of these landforms and relate them more confidently to the Paleozoic stratigraphy of the region. In this paper we reevaluate Thwaites' speculations about the age and origin of these landforms.

Description

The Baraboo Hills

The geology of the Baraboo Hills has been outlined by Dalziel and Dott (1970) and Clayton and Attig (1990). In the area surrounding the Baraboo Hills, Paleozoic rock lies on a generally flat unconformity on Precambrian rock. Before the Paleozoic sediment was deposited, the Baraboo Hills rose more than 350 m above the surrounding plain (Fig. 2). Then, as now, the hills were made up of quartzite of the Baraboo Formation, which was more than 1.5 km thick. The quartzite consists of quartz sand that underwent low-grade metamorphism to produce a rock that is highly resistant to erosion. The Baraboo Formation was folded into a doubly plunging syncline, resulting in the oval pattern of hills shown in Figure 1b. The north and south halves of the oval are called the North Range and the South Range, respectively.

The Baraboo Hills then were buried with quartz and lime sand during Late Cambrian and Early Ordovician time. At least the top of the South Range was reexposed by erosion during Middle Ordovician time, and the hills again were buried during Late Ordovician time, beginning with the quartz sand of the St. Peter Formation. By Late Paleozoic time, an additional few hundred meters of marine sediment had probably been deposited on top of the hills. Marine deposition had ceased by late Pennsylvanian time (Shaver et al. 1985). During the ensuing 200 million years, the land surface was lowered to near the level of the top of the Baraboo Hills.

The summit of South Range probably was exposed again just before the fluvial gravel of the "Windrow Formation" was deposited on one of the highest parts of the South Range, above the East Bluff of Devils Lake (Fig. 1c; Thwaites and Twenhofel

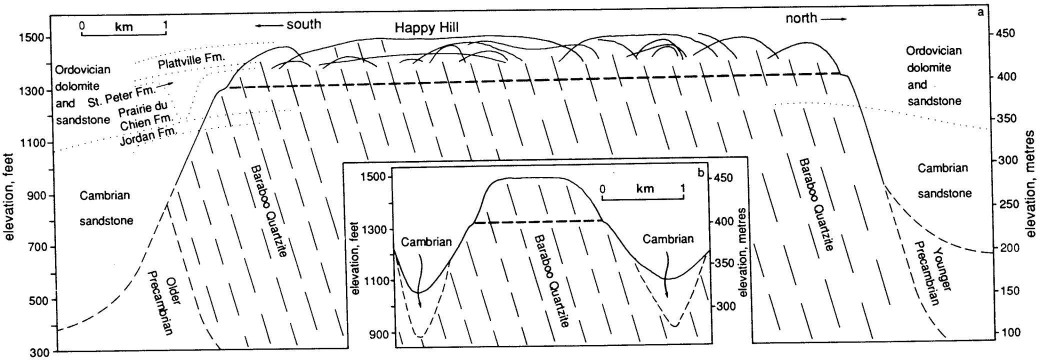

Fig. 2. **a**: Composite profile of summit plateaus of the South Range (the thin, solid lines at the top of the diagram), viewed from east to west. Vertical exaggeration x 10. The position of the subsummit benches is shown with a heavy dashed line. The thin dashed lines in the Baraboo quartzite indicate dip of the quartzite. The Precambrian, Cambrian, and lowest Ordovician stratigraphy shown at the north and south flanks of the range is based on local information, but the Platteville Formation has been projected from an area 40 km farther south. **b**: Cross section through a representation plateau, with flanking valleys and valley fills (middle of the South Range; sec. 17, 20, and 28, T11N, R6E).

1921, 296–97). It is unknown when that event occured, but guesses have generally ranged from Early Cretaceous to Pliocene (Thwaites and Twenhofel 1921, 307–10; Andrews 1958; Anderson 1988, 255–56). The landscape surrounding the Baraboo Hills since then has been lowered about 60 m at the west end, 250 m at Devils Lake (Fig. 1c; WGNHS Geologic Logs Sk-17 and Sk-39), and 300 m at Portage near the east end of the hills (Fig. 1b; WGNHS Geologic Log Co-634). The stratigraphic relationships summarized here and shown in Figure 2a indicate that the Baraboo Hills are much the same shape today as they were in Middle Cambrian time.

Valleys

The North and South Ranges of the Baraboo Hills are irregular quartzite ridges cut by gorges and valleys. The gorges have been cut completely through the ranges. They had a complex history, including considerable Pleistocene erosion when they functioned as spillways of glacial Lake Wisconsin (Clayton and Attig 1989); they will not be further discussed.

In contrast, the valleys head within the ranges. The largest valleys in the unglaciated part of the South Range are marked by *X*s in Figure 1c. These are a few kilometers long, about 1 km wide, and about 100 m deep. They tend to be of uniform width and abruptly terminate at broad, rounded valley heads. The valleys are walled with Baraboo quartzite, but their bottoms are generally underlain by 20 to 60 m of Cambrian sandstone and conglomerate (Fig. 2b).

Subsummit Benches and Scarps

Nearly flat benches have been cut into the Baraboo quartzite on the sides of each of these valleys (Fig. 1c, 2a, and 2b). The benches are typically a few tens of meters wide. Above the bench is a scarp with a slope of about 20°. Below the bench, the valley side typically slopes about 10° to 15°. The benches are about 30 m below the edge of the summit plateaus (Fig. 2a), and are at nearly the same elevation throughout the South Range, descending slightly to the south at about 1 m/km; they are at an elevation of about 402 m (1320 ft) on the north side of the South Range and at about 393 m (1290 ft) on the south side.

The benches are generally covered by forest, but, even so, in many places they are obvious from a distance (Fig. 3a). In addition, they are generally conspicuous in the few places where crossed by roads, especially when leaves are off the trees and patches of snow remain on the bench after a thaw. The benches can be seen where Freedom Road descends from the summit plateau on the south side of Happy Hill (4 km northeast of the community of Denzer) and at the junction of Tower and Denzer Roads (6 km north of Denzer; Fig. 3b).

Summit Plateaus

The highest hill tops in the unglaciated part of the South Range are remarkably flat (Fig. 2a, 2b, and 3c). These summit plateaus are typically about 0.5 km wide, with a maximum width of 1.5 km and a maximum length of 7.5 km (Fig. 1 and 2). The middles of the plateaus, at elevations between about 430 m (1410 ft) and 454 m (1490 ft), are horizontal, with slopes increasing to several degrees near the edge, at elevations between about 421 m (1380 ft) and 433 m (1420 ft). The plateaus are quartzite overlain by a few meters of yellowish-brown silt and clay containing quartzite fragments. Thwaites (1935, 401; 1958, 147; 1960, 37–38) reported scattered loose fragments of Paleozoic chert on the plateau surface, as well as a few small exposures of in-place lower-Paleozoic conglomerate along the edge of the plateaus.

Age and Origin

Valleys

Most large valleys in the South Range are known to have formed before Late Cambrian time, because there is Late Cambrian sandstone and conglomerate in the valley bottoms (Fig. 2b; Dalziel and Dott 1970). The valleys are known to have been at least 20 to 60 m deeper at the beginning of Late Cambrian time than they are today, because the Late Cambrian fill is that thick, and the interfluves may have been considerably higher, if the summit plateaus were eroded in Ordovician time, as will be discussed. Otherwise, the general shape of the valleys probably has changed little, because thin patches of Cambrian rock occur in a few places high on the valley walls (Thwaites 1935, 401; Thwaites 1958, 147; Thwaites 1960, 38).

Most large valleys in the unglaciated part of the South Range are shaped like typical stream valleys. They require no explanation other than hillslope and stream erosion through Early and Middle Cambrian time and perhaps also during latest Precambrian time.

Subsummit Benches and Scarps

The subsummit benches on the South Range are not structural terraces, because they slope only about 1 m/km (less than 0.1°) but are cut in quartzite that dips 10° to 40° (Fig. 2). These are not fluvial terraces because they slope to the south, whereas the valleys slope north and south on either side of the range. Thwaites (1935, 401; 1958, 147–48; 1960, 38–39) concluded that these benches and the scarps above were cut into the quartzite by marine shore erosion. We agree, because no other explanation seems

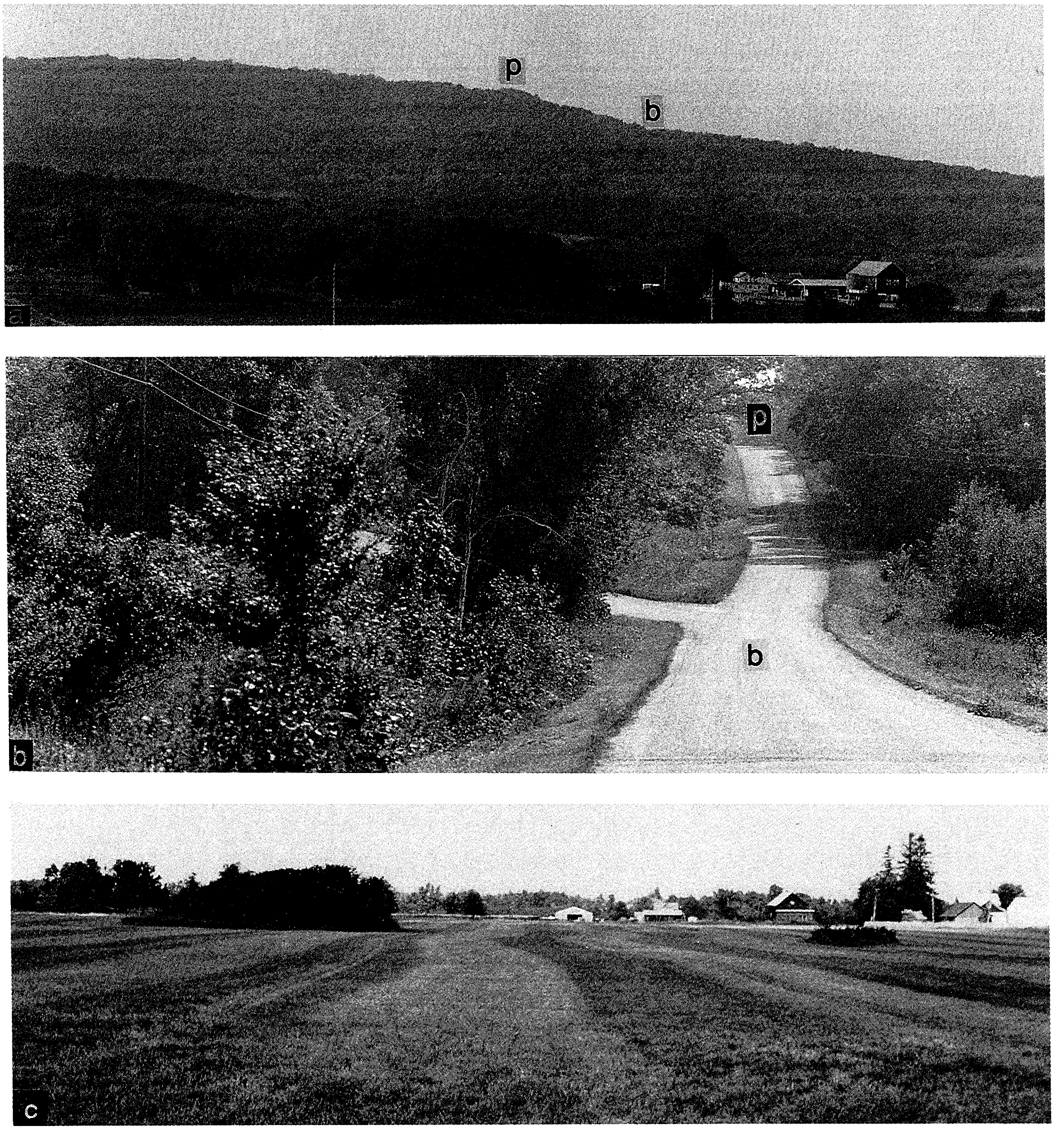

Fig. 3. **a**: North edge (p) of the summit plateau northeast of Happy Hill (Fig. 1c), with subsummit scarp (p-b) and bench (b); taken west-northwestward from middle of NE ¼ sec. 22, T11N, R6E. **b**: West edge (p) of the summit plateau of Happy Hill, with subsummit scarp (p-b) and bench (b); taken southward at southwest corner of SE ¼ SW ¼ sec. 27, T11N, R5E. **c**: Summit plateau of Happy Hill; taken northward from the south edge of the SE ¼ SE ¼ SE ¼ sec. 26, T11N, R5E.

plausible. However, the scarps clearly have been rejuvenated in places by mass movement when permafrost was present during the Pleistocene (Clayton and Attig 1990).

Although there is no direct stratigraphic evidence, these shore benches were most likely cut during the Ordovician. Patches of early Paleozoic conglomerate occur locally on the slope just below the benches (Thwaites 1958, 147; Thwaites 1960, 38). The formations present on either flank of the South Range can be projected into the range (dotted lines in Fig. 2a), using the stratigraphic and structural information of Clayton and Attig (1990, Plates 1 and 2, Fig. 13 and 14); the contact between the Jordan Formation (Late Cambrian) and Prairie du Chien Formation (Early Ordovician) is about 30 m below the benches. The original thickness of the Prairie du Chien here is unknown, but it is 60 m thick 40 km to the south (WGNHS Geologic Log Dn-993) and may have been that thick across the South Range. If the Prairie du Chien dolomite was deposited near sea level on the Baraboo Hills, the benches would have been cut before the upper Prairie du Chien was deposited, during Early Ordovician time, as suggested by Thwaites (1935, 401; 1958, 147; 1960, 38). This conclusion is corroborated, in a general way, by the dip of the benches; as shown in Figure 2a, the benches slope southward about 1 m/km, about the same as the regional dip of the Prairie du Chien Formation in the Baraboo area (Clayton and Attig 1990, Fig. 14).

If the benches were eroded at that time, much eroded quartzite would be predicted to occur in the upper part of the Prairie du Chien Formation. However, we know of no sedimentological evidence for increased erosion and deposition of quartzite around the Baraboo Hills at that time, because appropriate exposures are unavailable—no more than about the lower 25 m of the Prairie du Chien Formation is exposed in the Baraboo region.

Other less conspicuous benches and scarps occur at lower elevations on both the North and South Ranges. Wanenmacher (1932, 75–76) and Raasch (1958) interpreted these as marine shore terraces formed in Late Cambrian time, and we agree with this interpretation.

Summit Plateaus

If the top of the South Range had been rounded or marked by a series of hogbacks over harder layers in the northward-dipping quartzite, the shape of the range would require little explanation other than normal subaerial erosional processes operating over a long period of time. However, the summit plateaus, crosscutting the dipping quartzite, require some special explanation. Before Thwaites studied them, the summit plateaus were considered the remnants of a peneplain, or at least of a subaerial erosion plain.

Martin (1916, 68) and Smith (1931, 128), and others, thought this was a peneplain cut in Precambrian time. Thwaites (1935, 398; 1958, 141; 1960, 37), however, thought the plateaus were cut after Precambrian time, doubting that the Precambrian surface surrounding the Baraboo Hills could have been lowered 350 m without destroying the erosion-surface remnants on the hills. Furthermore, the summit plateaus seem to slope southward at about the same inclination as the subsummit benches and the Prairie du Chien Formation (1 m/km; Fig. 2a); if the summit plateaus were cut before the Precambrian plain surrounding the Baraboo Hills, they should slope south at least as steeply as that plain (2 to 4 m/km; Thwaites 1957).

Others, such as Trowbridge (1917, 352–53), suggested that the summit plateaus are remnants of a plain (the "Dodgeville peneplain") cut by subaerial processes when the South Range was being exhumed in Mesozoic or Cenozoic time. Thwaites (1935, 403; 1958, 149; 1960, 37) argued that if subaerial erosion was capable of planing the extremely resistant quartzite, erosion should also have been capable of planing the much weaker Paleozoic dolomite and shale of Blue Mounds (40 km south of the Baraboo Hills), one of which is 70 m higher than the South Range. Thwaites argued further that scattered loose blocks of Paleozoic chert on the plateaus are an indication of much less erosive activity than would have been required to plane the quartzite from the top of the South Range. The patches of lower-Paleozoic conglomerate on the plateaus also indicate they could not have been formed in Mesozoic or Cenozoic time.

As indicated in the discussion of the subsummit benches, if the formations on either side of the South Range are projected into the range (Fig. 2a), the position of the middle Ordovician unconformity (at the base of the St. Peter Formation) is unclear, but it may be near the level of the edges of the summit plateaus. This suggests the possibility that the summit plateaus were cut by subaerial erosion during this hiatus, which lasted about 25 million years (Shaver et al. 1985). This possibility suffers from none of the objections listed for Precambrian and post-Paleozoic subaerial erosion plains, but much less time was available. In addition, the summit plateaus seem too flat to correspond to the middle Ordovician unconformity, which is known to have considerable local relief near the Baraboo Hills; in some places the unconformity is as low as or even below the base of the Prairie du Chien Formation (suggested in left-hand side of Fig. 2a; Clayton and Attig 1990).

Thwaites (1931, 745; 1935, 401–02; 1958, 145–47; 1960, 36–38) suggested that the summit plateaus on the South Range are the result of marine shore erosion rather than subaerial erosion. Thwaites favored this interpretation for the following reasons. If subaerial erosion is ruled out, marine erosion is the only reasonable alternative, and marine shore erosion seems more capable of eroding the quartzite than any other process. Once the subsummit bench had been interpreted to result from shore erosion, it was reasonable to extend this interpretation to the summit plateaus. However, a shore plain might be expected to be even flatter than the plateaus on the South Range, although Thwaites suggested that sea level gradually rose as the plain was cut.

The age of the summit plateaus, if in fact they are marine shore terraces, is less clear than that of the subsummit benches. Thwaites (1935, 401; 1958, 147; 1960, 37) suggested that if the Paleozoic formations farther south are projected into the South Range, the summit plateaus would coincide with the base of the Platteville Formation (Late Ordovician). Our projection (Fig. 2a) shows this also, but because the original thickness of the Ordovician units is uncertain here, this projection could be in error. No sedimentological evidence is available for increased Platteville erosion and deposition around the Baraboo Hills, because there are no Platteville outcrops in the area.

Conclusion

The Baraboo Hills retain early Paleozoic landforms that have undergone little change since they were exhumed in Mesozoic or Cenozoic time. The large valleys in the South Range (except Devils Lake gorge) are normal stream valleys that formed before the Late Cambrian. The subsummit benches and scarps are almost certainly a marine shore terrace, which probably formed during the Early Ordovician. The summit plateaus are remnants of a plain formed by marine shoreline erosion or by subaerial erosion, possibly during either the Middle or Late Ordovician.

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Lee Clayton is a Professor and John W. Attig is an Associate Professor of the University of Wisconsin (Extension) at the Wisconsin Geological and Natural History Survey in Madison.

Philip A. Cochran, Martin E. Sneen,
and Alan P. Gripentrog

Notes on the biology of the American brook lamprey (Lampetra appendix) *in Wisconsin*

Abstract *American brook lampreys* (Lampetra appendix) *were collected from Taylor Creek in Rock County and were documented for the first time from Jambo Creek in Manitowoc County. Spawning at both sites occurred in early May at lower water temperatures (12–14°C) than previously recorded in Wisconsin. Although most spawning groups occurred in the open on gravel substrate, as is typically reported of spawning by lampreys, some spawning groups were found beneath cover. The sample of adult lampreys from Taylor Creek included a statistically significant excess of males. Adult male lampreys had relatively larger oral discs than females, whereas females displayed swelling along the leading edge of the second dorsal fin. A review of previous studies indicated that mean total lengths of adult males tend to be greater than those for females, although differences between means are rarely statistically significant at individual sites. Where the two species of nonparasitic lampreys have been collected from the same stream systems in Wisconsin, American brook lampreys occur upstream from northern brook lampreys* (Ichthyomyzon fossor*) significantly more often than vice versa.*

The American brook lamprey (*Lampetra appendix*) is widely distributed in eastern North America (Rohde 1980). Although it has been studied in other parts of its range (e.g., Hoff 1988; Lanteigne et al. 1981; Rohde et al. 1976; Seagle and Nagel 1982), little information on this species has been collected in Wisconsin (Becker 1983). Since the time that Becker's (1983) account was prepared, additional references to American brook lampreys in Wisconsin have been confined primarily to locality records (Cochran 1984; Fago 1982, 1983, 1984a, 1984b, 1985a, 1985b, 1986, 1992). The purpose of this note is to report new data on the biology of the American brook lamprey in Wisconsin, including several topics absent from or incompletely considered in Becker's (1983) account.

Methods

We collected adult lampreys in breeding condition at two sites. Taylor Creek is located in the Rock River basin (Mississippi River drainage) in Rock County (T2N, R10E, Sec. 30/31). At the site of capture, the West Church Road crossing, stream width was 4–5 m, the water was clear and up to 1 m deep, and the bottom was primarily sand, except for a concentration of rock slabs, cobble, and gravel beneath the bridge. Jambo Creek is a tributary to the East Twin River (Lake Michigan drainage) in Manitowoc County (T21N, R23E, Sec. 26). Stream width was 4–5 m, depth was 15–100 cm, and the water was clear with a slight reddish stain. Several gravel-bottomed riffles were present. American brook lampreys have been reported previously from Taylor Creek (Fago 1982) and from the East Twin River (Fago 1985b) but not from Jambo Creek (Fago 1985b).

Samples of lampreys were taken to the laboratory, where they were anesthetized with tricaine methanesulfonate (MS-222), measured for total length to the nearest mm, and weighed to the nearest 0.01 g. Oral disc lengths of lampreys from Jambo Creek were measured by pressing them flat against a transparent rule. Voucher specimens were placed in the University of Wisconsin-Madison Zoology Museum (Taylor Creek: UWZM 8432, Accession No. 84–77; Jambo Creek: UWZM 9951, Accession No. 91–176). Statistical analyses of morphological data were conducted with MINITAB (Schaefer and Anderson 1989).

It has been stated that American brook lampreys tend to be found upstream from northern brook lampreys *(Ichthyomyzon fossor)* when the two species occur in the same stream system (Morman 1979). We tested the applicability of this conclusion to Wisconsin waters with distribution maps provided by Fago (1983, 1984a, 1984b, 1985a). By overlaying transparencies of the maps for the two species, it was possible to tally cases in which one species occurred upstream of the other or vice versa. Deviations from random were tested through use of the binomial expansion (Sokal and Rohlf 1981).

Results

At Taylor Creek, 11 American brook lampreys were collected on May 4, 1984, at a water temperature of 14°C. All were captured beneath the bridge; 8 of the 11 were captured after a single individual was observed next to a rock slab and that slab was overturned. Ten of 11 lampreys were male, a result significantly different from expected under the null hypothesis that both sexes are equally abundant and equally vulnerable to capture (binomial test, $p = 0.012$). The males were readily made to express a rather transparent fluid from their urogenital papillae; the milt of spawning male American brook lampreys was described by Dean and Sumner (1897) as nearly colorless. Many individuals displayed the sorts of abrasions and other minor wounds that result from spawning activity.

At Jambo Creek, we observed spawning lampreys in 1988, 1989, and 1992. Several spawning groups were detected on May 2, 1988, but only one lamprey was found on May 4 at the same site. Water temperature was not measured on May 2, but was 16°C on May 4. In 1989, spawning groups were not observed on April 22, April 26, or April 30, but were present on May 3 at a water temperature of 13°C. All spawning groups were located just above riffles. Five groups were on open gravel substrate; individual group sizes were 6, 6, 7–10, 10–15, and 20–30. In addition, a group of ten lampreys was building a spawning depression beneath an overhanging stump, and a group of unknown size was building a pit beneath a large rock slab. Ten lampreys, five of each sex, were collected from among the spawning groups. On May 4, the lampreys had for the most part dispersed from the area occupied on the previous day; a single lamprey was observed beneath the stump that had sheltered a spawning group. Two spawning groups were located much further downstream. Water temperature remained at 13°C. In 1992, approximately 15 lampreys were observed over approximately 150 m of stream. All were in the open, and most were isolated individuals, but two pairs and one group of three were found in flat water just above riffles. Six females and three males were collected. Water temperature was 12°C.

The mean total length of the 30 American brook lampreys collected during this study was 160 mm (range: 139–187 mm). Mean body mass was 6.61 g (range: 3.83–11.27 g). Use of student's t-tests revealed significant differences between lampreys collected at Jambo Creek in 1989 and 1992 in mean total length ($t = 4.43$, $p < 0.001$) and mean body mass ($t = 4.52$, $p < 0.001$) (Table 1). Differences in mean total length and body mass between lampreys from Taylor Creek and Jambo Creek (1989 and 1992 data pooled) were not significant. For each of the three samples from Taylor and Jambo creeks, mean total length and body mass of male lampreys were greater than corresponding values for females (Table 1). When data for the three samples were pooled, the sexes were significantly different in both mean total length ($t = 2.81$, $p < 0.01$) and mean body mass ($t = 2.77$, $p = 0.01$).

The simple linear regression of the natural logarithm of body mass in grams (lnW) on the natural logarithm of total length in mm (lnL) was:

$$(1) \quad \ln W = -16.9 + 3.70 \ln L$$

($r^2 = 0.921$, $n = 30$). Analysis of covariance failed to reveal significant differences between regression lines calculated separately for the two sexes or for the two collection sites.

We measured the oral disc length of each lamprey from Jambo Creek and calculated relative disc length as the ratio of disc length to total length (expressed as a percentage). Total length was positively correlated with disc length ($r = 0.617$, d.f. = 17, $p < 0.01$). Analysis of covariance, with total length as the covariate, revealed a significant difference in disc length between the two sexes ($F_{1,16} = 12.53$, $p < 0.005$). This reflected a difference in mean relative disc length of males (5.83%, S.E. = 0.21%) and females (5.12%, S.E. = 0.13%). In addition to having relatively smaller oral discs, the Jambo Creek females displayed swelling along the leading edge of the second dorsal fin.

At Taylor Creek, American brook lampreys were collected with spotfin shiners (*Cyprinella spiloptera*), bluntnose minnows (*Pimephales notatus*), white suckers (*Catostomus commersoni*), banded darters (*Etheostoma zonale*), johnny darters (*Etheostoma nigrum*), and fantail darters (*Etheostoma flabellare*). At Jambo Creek, a designated trout stream, electrofishing on October 21, 1991, yielded the following species: brown trout (*Salmo trutta*), creek chub (*Semotilus atromaculatus*), common shiner (*Luxilus cornutus*), white sucker, black bullhead (*Ictalurus melas*), smallmouth bass (*Micropterus dolomieui*), green sunfish (*Lepomis cyanellus*), and mottled sculpin (*Cottus bairdi*). Only sculpins and young-of-the-year suckers were observed in large numbers.

We found 12 cases in which American brook lampreys and northern brook lampreys occurred together in the same stream

Table 1. Mean total length in millimeters and mean body mass in grams of American brook lampreys (*Lampetra appendix*) collected at Taylor and Jambo creeks, Wisconsin. Standard errors are in parentheses. All measurements were of living, anesthetized animals.

Locality	*Sex*	*Sample size*	*Total length (mm)*		*Body mass (g)*	
Taylor Creek	Male	10	161.5	(3.0)	6.80	(0.46)
	Female	1	158.0	—	5.48	—
	Both sexes pooled	11	161.2	(2.7)	6.68	(0.44)
Jambo Creek	Male	5	174.8	(4.9)	9.20	(0.84)
	Female	5	160.0	(2.1)	6.71	(0.47)
1989	Both sexes pooled	10	167.4	(3.5)	7.95	(0.61)
	Male	3	153.3	(1.3)	5.48	(0.17)
	Female	6	148.3	(2.3)	4.80	(0.25)
1992	Both sexes pooled	9	149.9	(1.7)	5.02	(0.21)
Both sites pooled	Male	18	163.8	(2.7)	7.25	(0.46)
	Female	12	154.0	(2.2)	5.65	(0.35)
	Both sexes pooled	30	159.9	(2.1)	6.60	(0.34)

(Fago 1983, 1984a, 1984b, 1985a). The American brook lamprey was reported further upstream in 10 of 12 streams. This result is significantly different from expected under the null hypothesis that the two species are equally likely to be found further upstream (binomial test, p = 0.039).

Discussion

Some generalizations about the temperature at which American brook lampreys spawn in the spring appear to be inaccurate. Becker (1983) stated that spawning in Wisconsin may begin at water temperatures of "about 17.2°C (63°F)." Robison and Buchanan (1988) cited Becker (1983) but inexplicably raised the temperature to "about 65°F (18°C) . . . ." In contrast, we observed spawning groups at temperatures of 12–14°C, and spawning at one site was apparently completed by the time water temperature had reached 16°C. Moreover, Cochran (1984) reported the occurrence of several spawning groups in Waukesha County at a water temperature of 15.4°C. While it is true that spawning by American brook lampreys in other parts of North America has been reported at temperatures as high as 20.6°C, most published accounts place the onset of spawning well below 15°C (Table 2).

Lampreys typically are reported to spawn in open, shallow, gravel-bottomed habitats. Cochran and Gripentrog (1992), however, reported that several species in the genus *Ichthyomyzon* aggregate beneath cover objects and sometimes spawn beneath cover. Our observations at both Taylor and Jambo

Table 2. Water temperatures at which American brook lampreys (*Lampetra appendix*) have been observed spawning.

Locality	*Temperature*	*Authority*
Wisconsin	12°C, 13°C, 14°C	This study
Wisconsin	15.4°C	Cochran (1984)
Michigan	17°C	Young & Cole (1900)
Michigan	First appear at 13–14.5°C	Okkelberg (1921)
Michigan	Mean of 14.1°C with a range of 6.7–20.6°C and a peak in one stream from 9.5–13.5°C	Morman (1979)
Quebec	8.3°–20.5°C with a peak at 17°C	Vladykov (1949)
Massachusetts	10–11°C	Hoff (1988)
New Hampshire	10–15.5°C	Sawyer (1960)
New York	10–18°C, but usually 15–18°C	Gage (1893, 1928)
New York	18.9°C	Dean & Sumner (1897)
Delaware	6.8–12.0°C	Rohde et al. (1976)
Tennessee	<15.5°C	Seagle & Nagel (1982)

creeks show that American brook lampreys also occasionally aggregate and spawn beneath cover objects. Young and Cole (1900) reported that nests may be situated beneath overhanging banks or logs.

In one of our samples of spawning-phase adults, males outnumbered females by a significant margin. Care must be taken when interpreting the literature on this topic. For example, Schuldt et al. (1987) cited Seagle and Nagel (1982) among authors who reported an excess of males, but Seagle and Nagel (1982) stated that the sex ratio was not statistically different from 1:1. Hoff (1988) and Scott and Crossman (1973) cited Young and Cole (1900) as reporting that males outnumbered females by a ratio of 5:1, but it was Dean and Sumner (1897) who reported that figure. Hoff (1988) reported that females outnumbered males 5:2, but with a sample size of 7, that result is not significantly different from 1:1 (binomial test, $p = 0.453$). Generally, however, adult male American brook lampreys outnumber females in collections made during or just prior to the spawning season (Dean and Sumner 1897; Young and Cole 1900; Kott 1971; Schuldt et al. 1987). Presumably, the sex ratio varies over time, since males are reported to precede females to the spawning site (Young and Cole 1900; Okkelberg 1921; but see Kott 1971).

Becker (1983) listed several traits for which American brook lampreys in Wisconsin are sexually dimorphic. Breeding males each have a long, threadlike urogenital papilla and relatively high dorsal fins separated by a sharp notch. Breeding females each have a prominent anal fin fold and relatively low dorsal fins separated by a broad notch. In addition, we report here that males have relatively larger oral discs than females and that the leading edge of the second dorsal fin in females may be swollen. A difference in disc size has been previously noted for American brook lampreys in Quebec (Kott

1974) and Delaware (Rohde et al. 1976); the larger discs of male lampreys may reflect their relatively greater role in nest construction (Beamish 1982). Swelling along the anterior margin of the female's second dorsal fin was mentioned by Gage (1928) and previously reported in several other species of *Lampetra* (Pletcher 1963; Larsen 1980; Hardisty 1986a, 1986b). Perhaps the swelling provides support for the body of the male, which during the spawning act fits into the notch between the first and second dorsal fins of the female (Breder and Rosen 1966).

Adult male American brook lampreys tended to be larger than females in our samples (Table 1). In each of five previous studies (Okkelberg 1921; Hubbs 1925; Sawyer 1960; Kott 1974; Rohde et al. 1976), mean total lengths of males were slightly but not significantly greater than those for females. However, if all paired samples for the two sexes were drawn randomly from populations with identical means, the probability of obtaining such a sequence of results is very low ($p = 0.0156$, binomial test). The apparently real trend for male American brook lampreys to be on average slightly larger than females is reinforced by the results of Schuldt et al. (1987), who obtained a mean total length for males slightly but significantly greater than that for females. Such a tendency may reflect a balance of opposing selective factors. Malmqvist (1983) and Beamish and Neville (1992), respectively, found that fertilization and spawning success declined as size differences between male and female lampreys increased; fertilization was most successful when the female/male length ratio was 1.05–1.14 (Malmqvist 1983). In contrast, Malmqvist (1983) and Becker (1983) reported behavior interpreted as fighting between male brook lampreys. The former results would select against substantial sexual divergence in size; the latter phenomenon would presumably favor larger males.

The tendency for American brook lampreys to be found upstream from northern brook lampreys reflects their preference for cooler temperatures (Scott and Crossman 1973), which are often associated with spring-fed headwaters. This pattern is not inviolate, however. Classical patterns of longitudinal zonation of stream fishes may be disrupted in drainages where springs empty cold water into the mid-reaches of streams (Swaidner and Berra 1979). Morman (1979) provided examples of inverted distributions of American and northern brook lampreys that apparently were related to reversed stream temperature gradients. An example of this phenomenon in Wisconsin may occur in the Mukwonago River (Cochran 1984). Northern brook lampreys were collected not far downstream from Eagle Springs Lake, the surface of which presumably warms quickly in the spring, whereas American brook lampreys were collected further downstream, below where a trout stream and numerous springs enter the river.

Wisconsin's native lampreys are not well understood by the general public (Cochran 1984) and may suffer through association with the sea lamprey (*Petromyzon marinus*), an exotic parasitic species that has caused great destruction of valuable fish in Lake Michigan and the other Great Lakes (Smith 1971). The American brook lamprey is nonparasitic and does not harm other fishes. Nevertheless, landowners along Jambo Creek informed us that they had encouraged a Cub Scout pack to catch and kill what they mistakenly thought were sea lampreys spawning on their property. (Spawning-phase sea lampreys from Lake Michigan do ascend the East Twin River to within 4 km of its confluence with Jambo Creek, but they are blocked by the Mishicot spillway from ascending closer.) We hope that further research on Wisconsin's native lampreys will help to dispel this sort of misunderstanding.

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__Philip A. Cochran__ is an Associate Professor of Biology at St. Norbert College. He is especially interested in the ecology and geographic distribution of lampreys and other fishes.

__Martin E. Sneen__ graduated from St. Norbert College in 1990 with a B.S. degree in Environmental Science. He currently works in Madison as an environmental consultant.

__Alan P. Gripentrog__ completed his B.S. degree in Environmental Science at St. Norbert College in 1988. He now works in Washington, D.C. for the Central Intelligence Agency.

Elisabeth R. Deppe and Richard C. Lathrop

Recent changes in the aquatic macrophyte community of Lake Mendota

Abstract *The aquatic macrophyte community of Lake Mendota was surveyed in the summers of 1989, 1990, and 1991 using a technique based on plant recovery on a rake. For comparison, more limited surveys were conducted during 1990 and 1991 on the other three lakes in the Yahara River Chain—Monona, Waubesa, and Kegonsa. For Lake Mendota, presence, relative frequency, and density of twelve species were determined. In 1989 and 1990, the Lake Mendota macrophyte community was dominated by* Ceratophyllum demersum L. *followed by* Myriophyllum spicatum L., *plants with biomasses especially heavy near the water surface. While the relative frequencies of these and other species remained nearly constant, almost all species decreased in density from 1989 to 1990. In 1991,* Ceratophyllum *declined again, and* Myriophyllum *became the most dominant. This same pattern was observed in Lakes Monona and Waubesa between 1990 and 1991. These density decreases were probably caused by especially poor spring and/or summer water clarity in 1990 in all three lakes. In Lake Mendota, this poor clarity resulted from an unusually long and dense blue-green algal bloom during May and June. Areas of high plant density along the west and southwest shorelines, including University Bay, showed the largest density decreases. This was probably due to an accumulation of algae in these regions, blown in by northeast winds during the crucial spring growth period. While Lake Mendota has been dominated by either* Myriophyllum spicatum *or* Ceratophyllum demersum *since the 1960s, our survey results indicate that plant densities can vary greatly in the short-term due to stochastic events.*

The submersed aquatic macrophytes of Lake Mendota, a calcareous 3,985-ha lake near Madison, Wisconsin, have been of interest to ecologists and lake managers for decades. Lake Mendota has undergone steady eutrophication since the mid-1800s, when its watershed was first developed (Lathrop 1992). Prior to the 1960s, the lake was dominated by wild celery (*Vallisneria americana* Michx.) and native pondweeds (*Potamogeton* spp.) (Lathrop 1989; Nichols et al. 1992). Since then, the plant community became less diverse, being dominated by Eurasian water milfoil (*Myriophyllum spicatum*). *Myriophyllum* was especially dense from the mid-1960s to the mid-1970s, when densities declined in Mendota and other Yahara River lakes (Monona, Waubesa, and Kegonsa) and Lake Wingra (Carpenter 1980; Lathrop 1989; Nichols et al. 1992).

Local lake managers continuously devote energy and resources to managing overabundant littoral biomasses of mainly *Myriophyllum*, particularly in Lakes Mendota, Monona, and Waubesa (Lathrop 1989). While providing important habitat for many fish species, this plant can become a nuisance to lakeside residents, boaters, and even anglers when growth is unchecked. In Lake Mendota, improved water clarity during 1986–88 caused ecologists and lake managers additional concern that *Myriophyllum* would increase in density and spread into deeper water.

To address these concerns, and because a systematic, detailed macrophyte survey had not been conducted on Lake Mendota since 1920 (Rickett 1922), the Wisconsin Department of Natural Resources (WDNR) undertook full shoreline surveys in the summers of 1989–91 to document the presence, relative density, and maximum rooting depth. The other three lakes in the Yahara River chain were also surveyed in the summers of 1990 and 1991 for comparison. The survey information should aid managers responsible for controlling overabundant macrophytes while indicating areas of native species deserving protection.

Methods

Field Survey

Lake Mendota's macrophytes were surveyed during the last two weeks of July and the first week of August in 1989–91. Plants were sampled along 47 transects positioned perpendicular to the shoreline at approximately 750-m intervals around the lake (Fig. 1). Transects were 300 m apart in University Bay, where we wanted additional data for historical comparison. Lakes Monona and Waubesa were surveyed in late June of 1990 and 1991 and Lake Kegonsa in early July of 1990 and 1991. Macrophytes were sampled along 13 evenly spaced transects in Monona (plus one in Monona Bay), 10 in Waubesa, and 8 in Kegonsa.

The surveys were conducted from a boat, which was moved between sampling stations designated at 0.5-m water depth intervals (0.5 m, 1.0 m, 1.5 m, etc.) on each transect until no vegetation occurred. Depths were determined using a measured pole in waters <3.0 m and a Lowrance FISH-LO-K-TOR depth-finder in waters 3.5–5.5 m. Each sampling station was subdivided into four quadrants, located off the front left, front right, rear left, and rear right of the boat. Each quadrant was then sampled by a single cast with a double-headed, weighted garden rake with a head width of 35 cm and 14 teeth, each 5 cm long. The rake was thrown into the water and dragged approximately 2 m across the bottom by means of an attached line. After the rake was pulled off the bottom it was flipped 180 degrees to ensure that plants snagged from the bottom would remain on the rake. This sampling technique for dividing stations into quadrants and collecting plants by rake casts followed Jessen and Lound (1962).

Plants collected on rake teeth were iden-

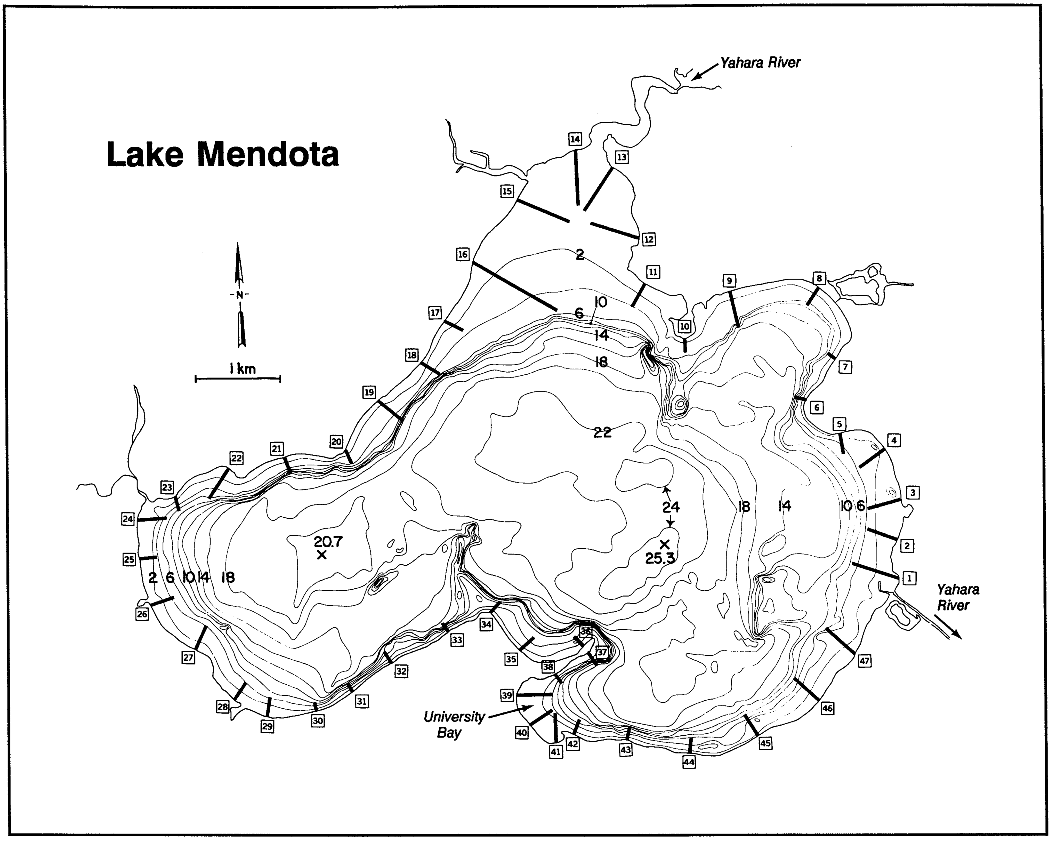

Fig. 1. Hydrographic map of Lake Mendota (with contours in meters) showing locations of the 47 study area transects.

tified following Fassett (1957) and Voss (1972). Whereas Jessen and Lound rated species on rake teeth only as present or absent, we developed a measure of estimating density as well. For each rake throw, a species was assigned a density rating from 0–5 based on the coverage of the upper rake head (both number of teeth and length of teeth covered). For example, species covering 1–20% of the rake head were given a rating of 1, species covering 21–40% were rated 2, etc. Ratings resulting from the four individual throws at each station were averaged to determine a density rating (DR) for each species. Further information on the rake survey method was provided in Deppe and Lathrop (1992). The simpler Jessen and Lound method of presence/absence on each rake was used for the 1990 surveys on Monona, Waubesa, and Kegonsa.

Statistical Analysis

Relative frequencies, which describe each species as constituting a certain percent of the whole macrophyte community, were computed for each lake. In addition, separate relative frequencies were computed for University Bay (transects 38–42) of Lake Mendota for the purpose of comparison with previous surveys only conducted in that area. Relative frequency for each species was calculated as the total number of rake casts on which a species appeared, divided by the total number of such encounters for all species. These calculations were based on data for all stations. While frequency of occurrence more accurately reflects a species distribution in a lake, we present only relative frequency information in this paper. Because different plant sampling methodologies were used in past surveys, only relative frequency data are directly comparable. However, it should be noted that relative frequency data were found to parallel frequency of occurrence data for Lake Mendota's macrophytes.

For Lake Mendota, density of plants is presented in two ways. Mean density ratings (MDRs) were calculated for the abundant and common species at each depth across all transects. In order to characterize the macrophyte community with respect to shoreline areas, density ratings of each species were summed for each transect and called their additive density ratings (ADRs).

Results

Macrophyte Community Composition

A total of ten submersed and two floating-leaved species were found in Lake Mendota during 1989–91 (Table 1). *Ceratophyllum demersum* (coontail) and *Myriophyllum spicatum* were the two most dominant species, each comprising 26–43% of the macrophyte community in 1989–91 (Table 1). Four other species—*Potamogeton pectinatus* L. (sago pondweed), *Vallisneria americana* (wild celery), *Heteranthera dubia* (Jacq.) MacM. (water stargrass), and *Elodea canadensis* Michx. (American elodea)—were common, each comprising 3–9% of Mendota macrophytes in 1989–91. The other six species were infrequently encountered (relative frequencies of each generally <1% in 1989–91). Composition of the macrophyte community in University Bay of Lake Mendota was almost the same as for the whole lake, dominated by *Myriophyllum* and *Ceratophyllum*, and containing seven of the other ten less abundant species found in Lake Mendota (Tables 1 and 2).

The macrophyte community of Lake Monona was very similar to Lake Mendota's, only lacking the two floating-leaved species and one uncommon *Potamogeton* (Table 1). Lakes Waubesa and Kegonsa were much less diverse, harboring only three species besides *Ceratophyllum* and *Myriophyllum.*

Abundant Species

Our Lake Mendota surveys document a transition from a *Ceratophyllum*-dominated macrophyte community to one dominated by *Myriophyllum. Ceratophyllum* was the most abundant species in 1989 and 1990, with higher relative frequencies and mean density ratings (MDRs) than *Myriophyllum* (Table 1 and Fig. 2). Both species experienced substantial decreases in density from 1989 to 1990 (Fig. 2). Densities of *Ceratophyllum* declined again in 1991, while densities of *Myriophyllum* remained nearly constant from 1990 to 1991, making *Myriophyllum* the most abundant species in 1991.

For both *Ceratophyllum* and *Myriophyllum*, areas of greatest abundance in 1989 exhibited the most dramatic decreases in density. In 1989, *Ceratophyllum* grew most densely along Lake Mendota's northwest and west shorelines and in University Bay (Fig. 3). Between 1989 and 1991, *Ceratophyllum* densities declined along the northwest shoreline and in University Bay by 68% and 95%, respectively. Relative frequencies in University Bay also portrayed a dramatic decrease in *Ceratophyllum* density from 1989

Table 1. Relative frequencies of macrophytes in Lake Mendota in 1989–91, and in Lakes Monona, Waubesa, and Kegonsa in 1990–91.

	Mendota			*Monona*		*Waubesa*		*Kegonsa*	
Species	*1989*	*1990*	*1991*	*1990*	*1991*	*1990*	*1991*	*1990*	*1991*
Submersed species									
Ceratophyllum demersum	42.5	42.4	26.4	43.2	10.1	43.0	10.2	5.4	9.5
Myriophyllum spicatum	34.1	32.0	40.9	41.4	61.2	41.8	60.2	83.9	82.5
Potamogeton pectinatus	6.8	8.5	8.3	2.5	14.5	3.5	2.3	8.9	3.6
Heteranthera dubia	5.8	5.5	7.1	0.9	3.5	4.1	5.5	–	0.8
Vallisneria americana	5.4	5.8	6.3	0.2	3.5	–	–	–	–
Elodea canadensis	3.6	3.3	7.0	1.3	1.8	–	–	–	–
Potamogeton crispus	0.7	0.5	0.9	10.1	2.6	7.6	18.0	1.8	3.6
Potamogeton richardsonii	0.5	0.4	0.6	0.4	1.8	–	–	–	–
Potamogeton zosteriformis	0.1	–	–	–	–	–	–	–	–
Potamogeton foliosis	–	0.1	1.5	–	1.0	–	–	–	–
Floating species									
Nymphaea tuberosa	0.3	0.3	0.8	–	–	–	–	–	–
Nelumbo lutea	0.3	1.1	0.2	–	–	–	–	–	–

to 1991 (Table 2). Along the south and southeast shorelines, areas of moderate *Ceratophyllum* density in 1989, densities dropped by 80% from 1989 to 1991. *Myriophyllum*, while fairly evenly distributed around the lake in 1989, was slightly more abundant in University Bay and along the west shoreline (Fig. 3). After decreases in nearly all regions from 1989 to 1990, sharpest in University Bay and along the west

Table 2. Percent relative frequency of macrophyte species in University Bay in selected years since 1966.*

Species	*1966*	*1978*	*1979*	*1980*	*1984*	*1989*	*1990*	*1991*
Ceratophyllum demersum	13.6	10.3	25.4	3.7	26.4	47.9	62.1	14.7
Myriophyllum spicatum	55.6	39.4	29.6	45.4	38.4	24.1	9.1	42.0
Vallisneria americana	15.7	14.3	14.8	14.2	1.2	8.9	8.3	8.7
Heteranthera dubia	1.2	–	–	1.0	–	11.3	7.6	7.3
Elodea canadensis	0.3	5.1	9.2	2.5	18.0	3.1	0.8	3.3
Nymphaea tuberosa	7.1	4.6	4.9	5.3	3.6	3.1	9.8	4.0
Nelumbo lutea	0.4	–	–	1.2	1.2	1.2	2.3	1.3
Potamogeton pectinatus	1.1	6.3	1.4	19.6	2.4	0.4	–	17.4
P. crispus	–	2.3	–	1.5	–	–	–	1.3
P. filiformis Pers.	–	0.6	10.6	–	–	–	–	–
P. foliosis	<0.1	15.4	4.2	2.0	–	–	–	–
P. nodosus Poiret	–	–	1.4	–	–	–	–	–
P. richardsonii	1.7	–	–	0.9	–	–	–	–
P. zosteriformis	0.1	–	–	–	–	–	–	–
Najas flexilis (Willd.) Rostk. & Schmidt	0.1	0.6	–	1.0	–	–	–	–
Ranunculus trichophyllus Chaix	1.5	–	–	–	–	–	–	–
Zannichellia palustris L.	<0.1	–	- -	1.2	–	–	–	–
Unidentified spp.	–	–	–	–	7.2	–	–	–

*Data sources: 1966 (Lind and Cottam 1969); 1978–79 (raw data used by Andrews 1980); 1980 (Vander Zouwen 1982); 1984 (R. Lathrop, Wis. DNR, unpubl. data); 1989–91 (this study). All surveys were conducted during July–August.

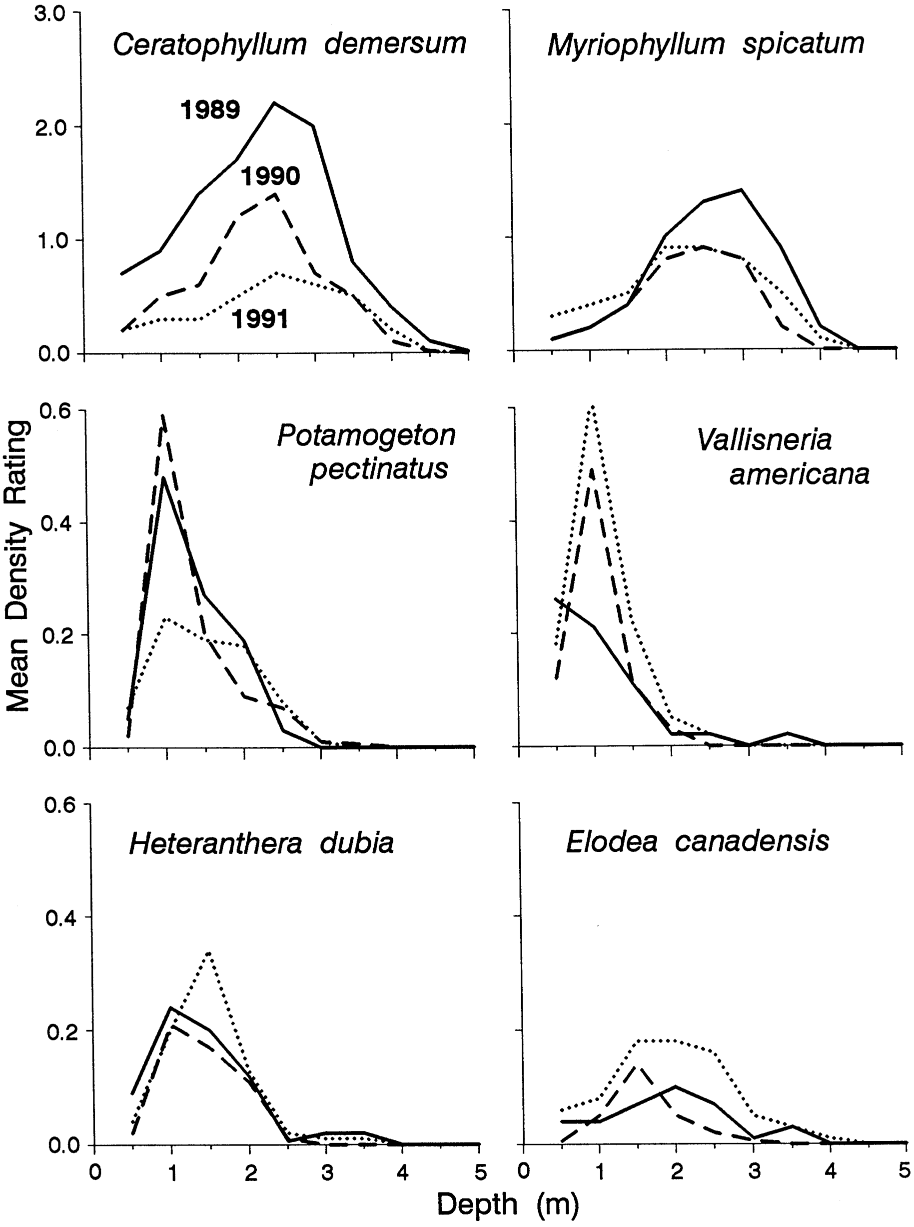

Fig. 2. Mean density ratings with respect to depth for abundant and common species in Lake Mendota, 1989–91. (Abundant species in top panels have scale 0–3.0; common species in middle and bottom panels have scale 0–0.6; 1989 – solid line, 1990 – dashed line, 1991 – dotted line.)

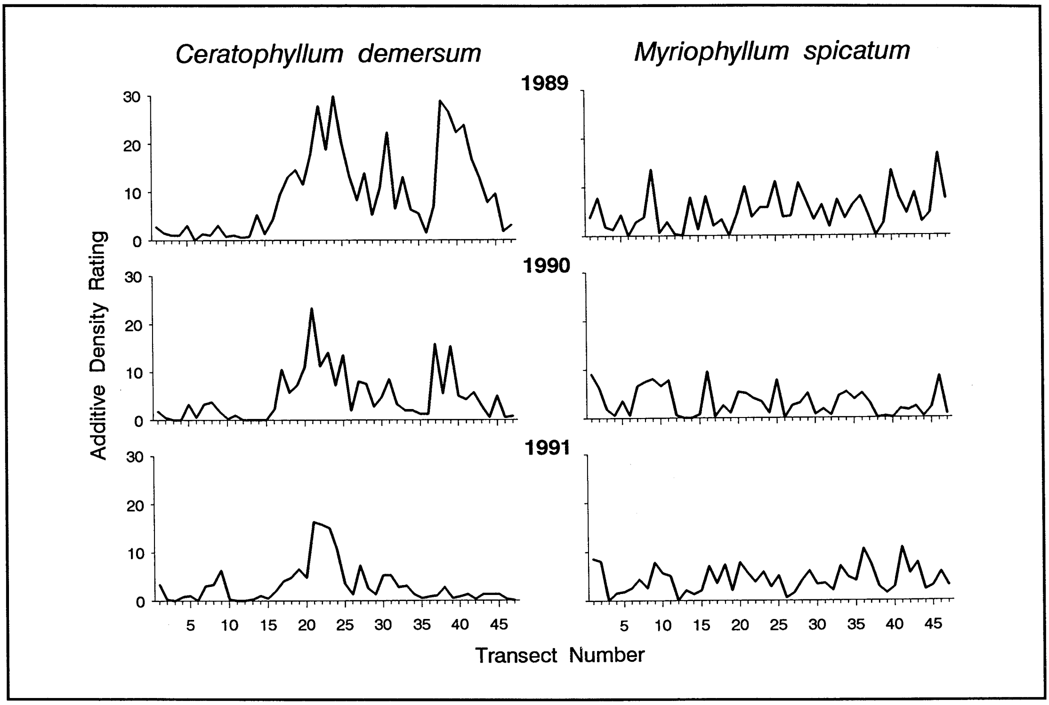

Fig. 3. Additive density ratings of *Ceratophyllum demersum* and *Myriophyllum spicatum* in regions of Lake Mendota and the percent change in these ratings from 1989–91. (University Bay = transects 38–41. See Figure 1 for other transect locations.)

shoreline, *Myriophyllum* densities almost regained their 1989 levels in 1991, unlike *Ceratophyllum*. During 1989–91, *Ceratophyllum* grew most densely between 2.0 m and 3.0 m of water depth, and *Myrophyllum* between 2.5 m and 3.0 m (Fig. 2).

In Lakes Monona and Waubesa, *Ceratophyllum* dominated in 1990 but dropped dramatically in relative frequency in 1991, while *Myriophyllum* frequencies increased (Table 1). Relative frequency for Lake Kegonsa, a lake with much sparser macrophytes, was almost totally dominated by *Myriophyllum* in both 1990 and 1991.

Common Species

The four common submersed species—*P. pectinatus*, *Vallisneria*, *Heteranthera*, and *Elodea*—were found less frequently and in lower densities than *Ceratophyllum* and *Myriophyllum* at all water depths, but grew most abundantly in shallower depths (< 2.0 m) (Table 1 and Fig. 2). In 1989, *Vallisneria*, *Heteranthera*, and *Elodea* had peak MDRs at depths of 0.5–1.0 m, 1.0–1.5 m, and 1.5–2.0 m, respectively. Small differences in MDRs occurred during the three years for these four species, but no consistent trend was evident. They were generally found at transects scattered all over the lake, with some prevalence on certain shorelines. Distribution of *P. pectinatus*, although fairly uniform in 1989, seemed less random than the others. It was entirely absent from University Bay in 1990; however, its greatest densities occurred there in 1991, reflected by its relative frequency of 17.4% (Table 2).

ERRATA

Elisabeth R. Deppe and Richard C. Lathrop. 1993. "Recent changes in the aquatic macrophyte community of Lake Mendota." ***Transactions of the Wisconsin Academy of Sciences, Arts and Letters*** **81: 47-58.**

Because of a change in font made by the printer at the final typesetting, the ≤ symbol was lost, causing a major problem in data interpretation on page 55.

Please note the corrections indicated on the proof reproduced on the back of this sheet and transcribe them onto page 55 of your 1993 *Transactions* volume so that future problems with data interpretation can be avoided.

(over)

Uncommon Species

In the three survey years, six species were found very infrequently and at very low densities in Lake Mendota: *Potamogeton crispus* L., *P. richardsonii* (A. Benn.) Rydb., *P. zosteriformis* Fern., *P. foliosis* Raf., *Nelumbo lutea* (Willd.) Pers., and *Nymphaea tuberosa* Paine (Table 1). In 1989 and 1990, *P. crispus* was found at low densities on transects off the eastern and northern shorelines, while in 1991 it was found almost exclusively along the west and south shorelines. In all three years, *P. richardsonii* was found in moderate abundance at transect 45 and more sparsely at a few other transects during 1989–91. For all three years, the two floating-leaved lily species *Nelumbo lutea* and *Nymphaea tuberosa* grew densely at ≤1.0 m in University Bay at transect 39, and elsewhere in the bay at varying densities from 1989–91. These species were also found along the east shoreline at transect 47 in 1989. *P. foliosis* was found at scattered sites in 1990–91, and *P. zosteriformis* was found at only one station in 1989.

Depth Limit of Growth

The depth limit of plant growth in Lake Mendota was somewhat variable between transects but generally occurred between 3.0 and 4.0 m for 1989–91 (Table 3). Depth limits shifted to slightly shallower ranges in 1990, but returned to near-1989 levels in 1991. Depth limit decreased by 0.5 m from 1989 to 1990 at all transects in University Bay and along the northwest shoreline where plant growth was densest.

Depth limit of plant growth in Lake Monona generally occurred at 3.5 m in 1990, but at 2.5 m in 1991. Similarly, in Lake Waubesa these figures went from 3.0 m in 1990 to 2.0–3.0 m in 1991. In Lake Kegonsa, depth limits increased from 2.0–2.5 m in 1990 to 3.0 m in 1991.

Because most plant growth occurred at ≤3–4 m in Lake Mendota, it is noteworthy that 10% of stations ≤3 m in 1989 were devoid of plants, while 20% had no vegetation in 1990 and 1991. In 1990, 7% and 1% of stations ≤3 m were without vegetation in Monona and Waubesa, respectively, but this increased to 30% and 48% for the two lakes in 1991. In Lake Kegonsa, 58% of stations ≤3 m were without macrophytes in 1990, but only 21% in 1991.

Discussion

Depth Distribution

In our 1989–91 surveys in Lake Mendota, macrophytes were found almost entirely at water depths between 0.5 and 3.5 m, while certain depths favored growth of particular species. *Ceratophyllum* and *Myriophyllum spicatum*, tall-growing plants with biomasses heaviest near the water surface, grew most densely between 2.0 and 3.0 m. The common species, tending not to grow as tall, were found largely between 0.5 and 2.0 m, where they can receive adequate light. Their infrequent occurrence in water depths >2.0 m suggests that they may be shaded by algal blooms and dense growths of *Ceratophyllum* and *Myriophyllum*. Lack of macrophyte growth at the 0.5 m contour is probably due to one or more of the following reasons: rocky substrate, more pronounced wave action, ice shifting in winter, and the controlled lowering of the lake level over the winter months.

Macrophyte Community of University Bay Since the 1960s

Myriophyllum spicatum dominated the plant community from its introduction in the

(over)

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Table 3. Depth limits of macrophyte growth in Lake Mendota in 1989–91.

Sampling Station (m)	*No. transects where plants ceased*					
	1989		*1990*		*1991*	
0.5	0		0		0	
1.0	0		0		1	(2%)
1.5	0		0		0	
2.0	0		1	(2%)	2	(5%)
2.5	3	(7%)	2	(5%)	5	(12%)
3.0	12	(29%)	12	(28%)	8	(18%)
3.5	13	(31%)	20	(47%)	15	(35%)
4.0	9	(21%)	7	(16%)	11	(26%)
4.5	4	(10%)	1	(2%)	1	(2%)
5.0	1	(2%)	0		0	
Total	42*		43*		43*	

*Transects 12–15 at the Yahara River inlet were excluded in all years because of shallow maximum depths; transect 6 was also excluded in 1989 because no plants were found there due to rocky substrate

early 1960s until the mid-1970s, while *Potamogeton* spp. and *Vallisneria* declined (Table 2). *M. sibiricum* Komarov (native water milfoil, formerly called *M. exalbescens* Fern.), apparently disappeared (Nichols 1975) and has not been recorded in surveys through 1991. After the mid-1970s, relative abundances of *M. spicatum* declined while *Ceratophyllum* began to increase, with the exception of 1980. This decline in *M. spicatum* abundance following approximately a 10-year period of domination has been observed in other lakes including Lake Wingra (Carpenter 1980), although the reasons for this are unclear. Transient increases in narrow-leaved pondweeds such as *P. foliosis*, *P. filiformis* and *P. pectinatus* occurred between 1978 and 1980 in University Bay. However, by the 1980s, several pondweeds had either dropped dramatically in relative frequency or totally disappeared from the bay, indicating steadily declining diversity.

Our surveys indicate the general continuation of *Myriophyllum/Ceratophyllum* dominance, but the trend of increasing *Ceratophyllum* relative frequency observed through the 1980s was reversed in 1991. While both species experienced reductions in area of coverage, mean density, and maximum depth distribution from 1989 to 1990, *Cerato-phyllum* densities dropped again in 1991 (Figs. 2 and 3). *Myriophyllum* densities, however, remained nearly constant from 1990 to 1991. This reversal caused *Myriophyllum* to once again dominate, but at lower densities than were noted in the late 1960s or early 1970s.

Effect of Water Clarity

Water clarity can critically influence the densities, species composition, and maximum rooting depth of submersed aquatic macrophyte communities (Canfield et al. 1985; Chambers and Kalff 1985). In our surveys, it is most likely that the sudden shift to a *Myriophyllum*-dominated community may have been caused, at least in part, by a difference in the responses of *Ceratophyllum* and *Myriophyllum* to severely reduced light conditions in the spring of 1990. This situation was particularly pronounced in University Bay. During the spring of that year, an atypical heavy bloom of blue-green algae occurred in Lake Mendota that resulted in unusually poor water clarity when compared to other spring periods (Lathrop 1992, WDNR unpubl. data). Because prevailing winds were predominantly from the northeast during May, rather than the more typical southwestern winds for this season, the buoyant blue-green algae accumulated in the bay. Extremely poor water clarity resulted, at a time of year when young plants require adequate light to initiate growth from the sediments. Water clarity was poorer than normal for much of the remaining spring and summer months of 1990. By August of that year, the shore side of the sand bar in University Bay was almost completely devoid of submersed vegetation, and the plant densities of the entire bay were severely reduced. In 1991, the bay still harbored only sparse macrophyte growth, although *P. pectinatus* was much more abundant than usual (Table 2).

Poor spring water clarity in 1979 (Lathrop 1992) also affected the macrophyte community in University Bay. Andrews (1980) noted a decline in macrophyte abundance (particularly *Myriophyllum*) from 1978 to 1979. In 1980, Vander Zouwen (1982) found *Ceratophyllum* to be quite sparse when compared to earlier and later surveys. Interestingly, *P. pectinatus* also exhibited increased abundances one year after poor water clarity in both 1980 and 1991 (Table 2).

Poor spring and summer water clarity in 1990 also had an impact on the macrophyte communities of Lakes Monona and Waubesa. Both lakes exhibited huge drops in the relative frequency of *Ceratophyllum* from 1990 to 1991 as had occurred in Lake Mendota. Water clarity was typically poor for both 1990 and 1991 in Lake Kegonsa, where plants were sparse. Relative frequencies were similar in both years with *Myriophyllum* being the dominant plant.

While densities of the macrophyte community in Lake Mendota as a whole dropped as a result of poor water clarity in both 1979 and 1990, it is unclear why only *Ceratophyllum* declined a second year in a row (1980 and 1991). Future summer surveys will help document the ongoing changes that have occurred in Lake Mendota's macrophytes, particularly since the invasion of *M. spicatum*. It will be interesting whether the next few years will show a resurgence of *Ceratophyllum* and/or *Myriophyllum* or an increase in diversity.

Acknowledgments

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__Elisabeth Deppe__ was a limited term biologist with the Wisconsin DNR Bureau of Research, where she conducted macrophyte surveys of the four Yahara lakes in 1989, 1990, and 1991.

__Richard Lathrop__ is a limnologist with the DNR Bureau of Research. He has conducted research on the Yahara lakes since 1976.

James O. Evrard

Were wild turkeys found historically in northwest Wisconsin?

The restoration of the wild turkey *(Meleagris gallopavo)* in North America is one of wildlife management's great success stories. Once near extinction, the wild turkey now numbers approximately four million birds. The wild turkey's restoration in much of its historic range and successful introduction in other areas were accomplished by transplanting wild birds into suitable habitat.

With increasing interest in new environmental issues such as biodiversity and restoration biology, the technique of releasing wildlife species outside their historical range is being increasingly questioned. It is, therefore, important to accurately delineate the original distribution of wildlife species. This distribution in North America is generally accepted as that existing at the time of European exploration and settlement.

In Wisconsin, Schorger (1942) delineated the northern limit of the historical range of the eastern wild turkey *(M. g. silvestris)* as a line from Prairie du Chien to Green Bay (Fig. 1). Recent turkey range distributions (Hewitt 1967; Kallman 1987) continue to be based upon his work. In reaching his conclusions, Schorger disregarded or discredited two observations of wild turkeys near Lake Pepin, a natural widening of the Mississippi River about 100 miles north of Prairie du Chien and at the same latitude as Green Bay.

Schorger disregarded Father Hennepin's report that his party killed seven or eight large turkeys *(Cog d'Inde)* near Lake Pepin in 1680. Hennepin also mentioned that Indians reported bustards or wild turkeys *(Outardes ou* [or] *Cogs d'Inde)* in that area. In this instance, *Outarde* or bustard was synonymous with the turkey.

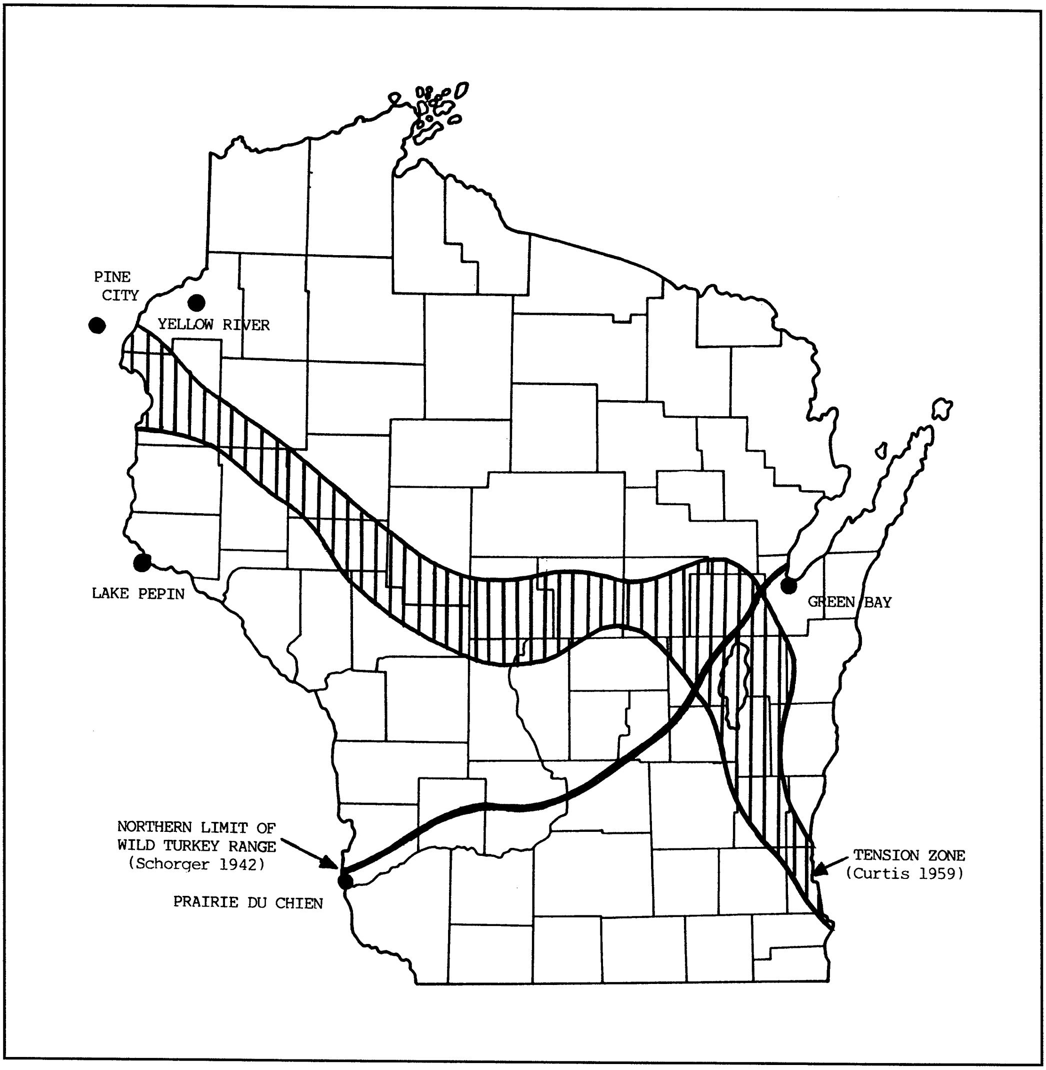

Fig. 1. Original range of the wild turkey delineated by Schorger (1942) and the Tension Zone of Curtis (1959).

Schorger discredited Jonathan Carver's 1776 observations of turkeys at Lake Pepin because he concluded they were pilfered from Hennepin's writings. However, Parker (1976) questioned the validity of the plagiarism charges. Carver's turkey observations may, indeed, be more valid than Schorger believed.

Schorger also attempted to make the case that *Outarde* was the French word for Canada geese *(Branta canadensis)* by using two observations east of Wisconsin, one from Lake Champlain in 1683 and the other from the mouth of the Cumberland River in 1795. However, he appeared to contradict himself by stating:

> Early explorers naturally would call the new American animals by the names of creatures in Europe that they resembled most closely. The *Outarde* or Bustard is a large stocky bird.

> The spreading of the tail and other phases of courtship demeanor give it a decided resemblance to the Turkey. Only speculation can be offered for the synonymy of *Outarde* and Canada Geese.

Two records not available to Schorger in 1942 indicate the wild turkey may have existed nearly 100 miles north of Lake Pepin (Fig. 1).

An *Outarde* was provided to the fur trader, John Sayer, by his Ojibway hunters at the North West Company post on the Snake River, near Pine City, Minnesota, on September 18, 1804 (Gates 1965). The fur trading post was located about 12 miles west of the St. Croix River in Pine County. The *Outarde* could not have been confused with geese because Sayer's journal also mentions that he received geese from his hunters six days later and on five subsequent occasions.

The second record consisted of a wild turkey bone found in a refuse pit during an archeological excavation of a combined North West Company and XY Company fur trading post on the Yellow River in Burnett County, Wisconsin (Ewen 1983). The post was occupied during the winters of 1802–03 and 1804–05 and was located about 3 miles from the St. Croix River and about 28 miles east of the contemporary Snake River post. Journal entries from both forts (Gates 1965; Thwaites 1911) indicated that hunters took their game within 20–30 miles of the posts, suggesting turkeys were present in Pine and Burnett counties at that time.

How could the wild turkey have existed nearly 200 miles north of the original range outlined by Schorger?

A review of presettlement vegetation and the location of the "tension zone" in Wisconsin, a transitional boundary between northern and southern plant and animal communities described by Curtis (1959), supports the northern turkey records. Oak forests and prairies—both turkey habitat—were found south and west of the tension zone (Fig. 1). Oak forests and remnant prairies still cloak the Mississippi River bluffs from the Illinois border to the Minnesota border and along the St. Croix River north into Burnett and Pine counties.

If suitable turkey habitat existed in the Mississippi and tributary river valleys north of Prairie du Chien, why were there so few historical turkey records for the area?

A potential answer to this question was given by Schorger himself. He stated that the northern range limit of the wild turkey, like the bobwhite quail *(Colinus virginianus)* and prairie chicken *(Tympanuchos pinnatus)*, occurred in Wisconsin. He speculated that prior to European settlement, these species existed as members of Wisconsin's fauna only by periodic replenishment from Illinois. The northern limit of their range varied in response to the severity of winter weather, moving northward during a succession of mild winters and retreating southward following severe winters.

Schorger reasoned that the scarcity of wild turkey records in Wisconsin for the last half of the nineteenth century was primarily due to the severe winter of 1842–43 when the species was nearly extirpated in the state. Southern and western Wisconsin were not settled by Europeans until the 1850s so there were very few turkeys remaining for the settlers to see. Massive habitat destruction and unregulated hunting that accompanied settlement sealed the fate of the few remaining turkeys.

Kumlien and Hollister in 1903 stated:

> The Wild Turkey is to-day so rare in Wisconsin that it is safe to say that it is extinct. Authentic references are meager and fragmentary. Dr. Hoy and others say it was abundant in southern Wisconsin prior to 1840. Several references, of which Hoy's is one of the most

> reliable, state that the winter of 1842 was practically fatal to them.

Shorger quoted Dr. Hoy concerning the near extinction of the turkey in Wisconsin:

> I am told by Dr. E. B. Wolcott that turkeys were abundant in Wisconsin prior to the hard winter of 1842–43, when snow was yet two feet deep in March, with a firm crust, so that the turkeys could not get to the ground; they hence became so poor and weak that they could not fly and so were an easy prey for the wolves, wildcats, foxes and minks. The Doctor further stated that he saw but one single turkey the next winter, and none since.

Shorger stated that the winter of 1842 was known as the "hard winter" for decades afterward.

There were other hard winters that affected wild turkeys, both historically and more recently. Schorger quoted from the diary of Marquette that the winter of 1674 was one of intense cold and deep snow at the present site of Chicago, Illinois. On December 12, Marquette wrote:

> We contented ourselves with killing three or four turkeys out of many that came around our cabin because they were almost dying of hunger.

Schorger concluded that since these conditions existed at Chicago, it was probable that most wild turkeys in Wisconsin perished that winter.

A more recent example is given by Robbins (1991). Wild turkeys released in the Meadow Valley area of central Wisconsin in the mid-1950s increased to 2,500 birds a decade later. However, the winter of 1968–69 was one of deep snow which took a heavy toll of turkeys. By 1973, the estimated population was only 70 birds.

With this in mind, delineating the historical range of the wild turkey in Wisconsin would depend upon the time period examined. Few turkey records for the northern edge of its range would be found for years following an exceptionally severe winter. Conversely, one could expect to find more wild turkey records during an extended period of mild winters.

European settlement prevented the natural ebb and flow of the northern limit of the occupied wild turkey range and eliminated the species in Wisconsin. But the conversion of much of the state's turkey habitat to agricultural uses set the stage for the eventual reestablishment of the wild turkey. The availability of waste corn in harvested fields and spread manure on today's farms provide winter food that was unavailable to turkeys before European settlement. Wild turkeys can now survive severe winters that would have been impossible in the past.

The wild turkey has returned to the area in east-central Minnesota and northwest Wisconsin where it was found in 1804. Birds released about ten miles south of Pine City, Minnesota, in the 1980s reproduced and spread northward and eastward, crossing the St. Croix River into Burnett and adjoining Polk counties, Wisconsin. The turkey population in this area of Wisconsin in the spring of 1992 was estimated to be 100–200 birds (Michael Johnson, Wisconsin Department of Natural Resources (WDNR), pers. comm. 1992). These birds survived the winter of 1991–92 despite snow depths of nearly 20 inches covering the ground more than five months.

It appears that the wild turkey is now a resident of northwest Wisconsin after an absence of nearly 200 years. The present population was bolstered by a release of wild-trapped turkeys from southern Wisconsin in early 1992. The WDNR plans an additional release of turkeys in the winter of 1992–93. Although severe winters may cause large population fluctuations, food supplied by current agricultural practices should ensure that scattered flocks will persist in this northern landscape.

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***James O. Evrard** is a wildlife research biologist for the Wisconsin Department of Natural Resources at Grantsburg.*

Marguerite H. Helmers

Creating the California Alps

John Muir, the nineteenth-century naturalist, was a prolific and elegant writer whose articles and books numbered in the hundreds through several revisions and editions. His nature writing combines the finest elements of scenic description with exciting adventure stories, but several of his short essays demonstrate much more: that certain styles of writing, like styles of clothing, painting, and music, are historically determined. Muir's writing obeys the conventions of the typical response to nature in the eighteenth and nineteenth century—appreciation of the sublime and the picturesque. This essay will trace Muir's uses of literary formulas of picturesque and sublime representation through two articles. These articles, "Snow-Storm on Mount Shasta" (1877) and "In the Heart of the California Alps" (1880), appeared during what Muir's literary biographer Herbert F. Smith refers to as Muir's "most fertile period," a time of discovery, experimentation, environmental activism, and written expression. They were published initially in *Harper's* and *Scribner's* magazines, although Muir later revised both for inclusion in his book *The Mountains of California* (1894).

These two short essays reveal also that Muir's writing is profoundly subversive. His efforts to incorporate description that would meet the demands of his leisure-class readers carries with it a touch of contempt at the passive mode of observation and conformity to convention that fostered those readers' demands. While he paints beautiful verbal pictures for his audience, inviting them to see the colors, shapes, and wonders of the mountains with him, he always leaves them behind as he moves, solitarily, into the frightful but enlightening adventures of the "California Alps." Literary biographers, including Herbert Smith and Michael Cohen, have noted the antagonism between

John Muir and the public. In many ways, this antagonism centered on a question of access. A solitary wanderer, Muir was fortunate to have access to the mountains, which enabled him to learn to study the peaks, in his words, "long and lovingly." It is such access that he wished to deny the tourists, fearing, like later preservationists, that sheer numbers of unappreciative humans would destroy the ecological balance and massive, expansive grandeur of the wild. Access requires railroads, coach roads, tour guides, walking paths, picnic grounds, in short, an entire institutional structure to accommodate viewing. These two essays reveal the conflict in his efforts to fashion the wilderness verbally, to encourage his readers that the wild was worth preserving, and yet to bar access to the pristine mountains of California. Muir's writings are a tourist's guide through the California mountains, through language and word-painting, but he is also in opposition to the aims of tourists and readers. He alone can find sublimity—a heightened experience—where others find views. While he followed established "rules" of scenic depiction in his writing, he used those rules to ridicule an audience of tourists and leisure-class readers who sought "fine scenes" in nature. My intent is to demonstrate the extent to which Muir employed verbal and artistic conventions in his writing and to show the degree to which these conventions carried an intentional, dual intent.

Herbert Smith contends also that Muir was a formula writer. Smith points to the fact that *Harper's Magazine* seemed to favor highly informational articles about exotic American subjects that could be illustrated nicely (H. Smith 80), such as stories about the wonders of nature. However, a more recent article by Michael Smith notes that Muir, like his fellow naturalist and writer Clarence King, was attempting to define a new style of writing, linking the scientific with the aesthetic (M. Smith 37). These two assessments are not mutually exclusive: while Muir sought to combine scientific writing, adventure, and scenic description, he still relied on specific aesthetic conventions in recreating the grandeur of the California Alps for his audience. Michael Smith's judgment points to an interesting point, however. Muir's writing in "Snow-Storm on Mount Shasta" and "In the Heart of the California Alps" is rather rough and experimental, at times awkward, and it is perhaps this roughness that has often caused biographers, critics, and admirers to turn to the revised versions in *The Mountains of California*. I believe, however, that these two early pieces give us a fresher look at the artist trying to mold his writing to the expectations of his audience while attempting to retain his own strong perspective.

The terms "picturesque" and "sublime" derive from painterly conventions dating from the eighteenth century. Literally, "picturesque" means bringing to nature the qualities of a picture. One of the foremost works of art criticism that deals with the picturesque is Christopher Hussey's *The Picturesque: Studies in a Point of View*. In that work, Hussey identifies the qualities selected by painters as elements of the picturesque:

> . . . roughness, lusciousness of texture, glinting, sparkling surfaces, the crumbling and decayed. These they found in the objects now known as picturesque: sandy lanes, dock leaves, gnarled trees, hovels, donkeys, and ruins. Their brushes were attracted to the rendering of these qualities, because they were well suited to paint. No moral feeling entered into the business, though sentiment was attached to many of these objects, particularly to rural scenes and ruins. (Hussey 246)

For painters (and, later, writers) who adopted its techniques, the picturesque became a way to moderate, to order, and to understand the wilderness of "the sublime." The sublime was, then, a rough and untamed version of wilderness, often frightening in its aspects. The picturesque aesthetically cultivated the raw landscape. Actual landscapes described as picturesque were ones in which life imitated the regularity of art, for the real was sought out for its most painterly qualities.

Hussey points out that the picturesque was "a practical aesthetic" prescribing rules to painters for observation and re-creation. The rules, which Muir applied to his writing, include: a scene composed of foreground, containing stock features such as rocks, cascades, broken ground, and ruins; a middleground, containing meadows and forests; off-skips, or side-screens, containing valleys, woods, rivers; and a background, consisting of perfectly pyramidal mountains and placid lakes (Hussey 116). Particular colors were in vogue. Greens were not allowed, while variations of brown were expected. Brown was associated with romance and sublimity, and because it is the season of browns, autumn became the season favored most by painters employing the picturesque (Hussey 43).

As Romantic poets turned to the picturesque and sublime for inspiration, certain words were intended to infuse language with the onomatopoetic sense of motion—of disorder breaking in on order. These were known as "words of high coloring" (Hussey 35). The presence of words like "shoot," "roll," "dash," "wrap," "bend," "rear," "stretch," "nod," "rage," "gush," "sweep," and "swell" became, like the color brown, another test for the presence of the picturesque (Hussey 35). Norman Foerster points out that Muir employed such onomatopoetic words frequently as a means of adding verisimilitude to what he described, and Foerster labels this Muir's "normal method" of writing (260).

Muir, in fact, combines words that evoke the sense of the picturesque and the sublime with painterly conventions of scenic arrangement. He composes the descriptions in these essays around orderly "scenes," often pausing in his narrative to point out to his audience the places where they may take in a picturesque view. It is not always easy to discern the differences between artistic conventions and literary conventions in his work, as there is a direct correspondence between the two. Conventional words of high coloring express the traditional tenets of picturesque and sublime painterly description. In her study of the intersection between Romantic poetry and conventions of representing nature, Marjorie Hope Nicolson has drawn attention to the ways in which Romantic poets depended on and perpetuated particular literary traditions of representing mountains, just as Muir chose specific words to evoke painter's qualities of color and form in California's Yosemite. Nicolson's work helps to illuminate the repetitions of standard scenic descriptions in Muir's two essays.

The progress of Muir's movements through the two narratives reveals an ascent from the easily comprehensible world of the picturesque to the awe-inspiring world of the sublime. Aesthetically, the picturesque was meant to have popular appeal. Virtually anyone could possess a "picturesque eye" (Hussey 83–84). The sublime, however, was a more exclusive experience, appealing to those with a "Romantic mind." While the picturesque eye could be easily enthralled by an arrangement of rocks and trees, the Romantic mind sought the moral implications of a scene. As Hussey writes, "The Romantic mind, stirred by a view, begins to examine *itself*, and to analyze the effects of the scenery upon its emotions. The picturesque eye, on the contrary, turns to the scene. . . ." (83–84).

In "Snow-Storm on Mount Shasta" and "In the Heart of the California Alps" Muir portrays himself as the possessor of a Romantic mind. In both of the essays, Muir is thrown by circumstances into dangerous situations which offer him the opportunity to reflect on the infinite. It is quite clearly implied in the essays that he alone is able to experience the sublime. While he often invites his readers to look upon a picturesque scene with him, he alone is forced into extraordinary feats of exertion that leave him pondering the workings of God in the world. Surrounded by boiling mud and noxious gases, the peak of the adventure story in "Snow-Storm," Muir seems almost cheerful to have the opportunity to contemplate "God's Design." He also records in "In the Heart of the California Alps" that when facing death atop Mount Ritter, hanging from a shard of rock, he is saved by a "Guardian Angel."

Muir constructs himself as the Romantic type, an exemplary mountaineer, insightful, sensitive, fearless, and self-sufficient. As Muir reveals in "Snow-Storm on Mount Shasta," he climbed mountains in shirt sleeves, packed no blankets, and, for sustenance, carried only a crust of bread and a tin cup with which to scoop water from mountain streams. Although he never mentions tourists in either of these articles, a knowledge of Muir's antagonism toward popular travel as documented in his letters and biographies sheds new light on his *ethos*, the way in which he constructs himself and reveals his attitude toward his audience. Travelers from the East, overburdened with clothing and provisions and blind to the true significance and potential danger of the wilderness around them, are conventional enough in themselves today, but Muir was working to fashion distinctions between those with a shallow perception of nature and those with a deeper understanding of nature, between those who were interested in the picturesque and those who were fascinated by the sublime. Fearful that the industries of farming and tourism would result in a desecration of wild spaces, Muir sought to portray to his audience the need to retain untouched spaces where the infinite might be experienced. In other words, as many people as possible had to remain behind on the path.

Muir's extraordinary sensitivity to the wilderness and his ability to experience the sublime workings of nature are shown to good advantage in "Snow-Storm on Mount Shasta," which is an unusual essay in that it combines an introductory section of scientific explication with picturesque descriptions and an adventure story. In the essay, Muir attends to the colors and contrasts of the landscape, introduces natural ruins, reflects with awe upon the powers of God, and directly appeals to the reader to behold scenes as picturesque. It is in "Snow-Storm on Mount Shasta" that Muir's efforts to combine scientific observation with literary writing seem most forced and awkward. Early in the essay, he divides the mountain into three botanic zones and enhances his verbal description with an illustration of three evenly concentric circles. He notes the elevation of each region and its indigenous flora and provides a list of all the coniferous trees he has discovered (Muir 523). The outermost zone, at the base of the mountain, is the chaparral zone, covered in evergreens and lilies; the inner zone, the fir zone, is covered in silver-firs; and the uppermost Alpine zone is covered in snow, dwarf pines, and some flowering plants. Following this catalogue, however, Muir shifts perspective, moving from a focus on the natural sciences to a focus on the aesthetic.

Muir opens the article by establishing the differences in texture, temperature, and tone between glacial ice and volcanic lava, contrasts which will figure prominently in the climax of the adventure story and which demonstrate nicely the desire to emphasize picturesque contrasts:

> Mount Shasta, situated near the northern extremity of the Sierra Nevada, rises in solitary grandeur from a lightly sculpted lava plain, and maintains a far more impressive and commanding individuality than any other mountain within the limits of California.
>
> Go where you will within a radius of from fifty to a hundred miles, there stands the colossal cone of Shasta, clad in perpetual snow, the one grand landmark that never sets. . . . During the glacial period Mount Shasta was a center of dispersal for the glaciers of the circumjacent region. The entire mountain was then loaded with ice, which, ever descending, grooved its sides and broke up its summit into a mass of ruins. (521)

Mount Shasta exhibits two qualities essential to sublime and picturesque description. Primarily, the mountain is introduced as a pyramid, part of the "backdrop" of the picture. The mountain is also irregular, broken into a mass of ruins. As Nicolson contends, irregularity began to replace the aesthetic of regularity in the late eighteenth century, when Addison praised the "rudeness" of the gardens in France and Italy in preference to the "regular," landscaped gardens of England (317). Acceptance of irregularity as a valid aesthetic quality gave new importance to the place of ruins in scenes. Nicolson notes that ruins were attractive because of their "asymmetry" (336). Muir describes the irregular summit of Mount Shasta as a mass of crumbled rock. It is, he writes, a natural "ruin."

The ruins and irregularity have further conventional associations, for Muir is careful to describe that they were formed by volcanic eruptions. Volcanoes were important to formulas of the sublime because the great geologic upheavals that they caused epitomized the ruining of nature: "The mountain bursts into flame, and man with all his works lies buried in the Ruins of Nature" (Nicolson 341). Ruins of nature reflected in turn on the frailness of human existence, which Nicolson refers to as the "Ruins of Time." Descriptive poets of the nineteenth century, most notably Byron and Shelley, shared the relish of earlier poets for thunderstorm and tempest, earthquake and volcanic eruption (Nicolson 380). Following the conventional literary usage of words of high coloring and the fascination with irregularity, ruins, volcanos, and natural violence, Muir paints Shasta's main summit. Viewing it from the north, he describes Shasta as:

> . . . an irregular blunt peaklet about ten feet high, fast disappearing before the stormy atmospheric erosion to which it is subjected. Hot sulphurous gases and vapors escape with a loud hissing noise from fissures in the lava near the base of the eastern ridge, opposite the highest peaklet. Several of the vents cast up a spray of clear bead-like drops of hot water, that ride repeatedly into the air and fall back until worn into vapor. (Muir 522–23)

As he begins the narrative portion of the essay—the story of his ascent of the mountain—he pauses to direct attention to the view from Strawberry Valley. It is the first direct appeal to the audience in the essay and suggests Muir's awareness of the leisured reader's demands for taking scenes. It is an awkward and theatrical intrusion into the narrative and an abrupt turning away from the concern with botanical taxonomies. With the potential for leisured readers to become inquisitive tourists, Cohen posits that "all of Muir's writings were for the tourists, since they involved the question of how to see. Most tourists did not want to hear philosophy, but wanted to know exactly where to stop and look" (Cohen 207). Muir, perhaps experimenting with what he saw as a necessity of the audience, caters to demands by writing that:

> . . . at Strawberry Valley there is a grand out-opening of the forests, and Shasta stands revealed at just the distance to be seen most comprehensively and impressively.
>
> Looking at outlines, there, in the immediate foreground, is a smooth green meadow with its crooked stream; then a zone of dark forest, its countless spires of fir and pine rising above one another higher and higher in luxuriant ranks; and above all the great white cone sweeping far into the cloudless blue. . . . (524)

The obligatory picturesque elements of this tri-level view are the meadow and (irregular) "crooked stream" in the foreground, the forest zone "rising above" the foreground as all well-painted middlegrounds and side-screens should, and the perfect pyramidal cone of the mountain, the focal point of the picture. Earlier in the essay, Muir had already written that Shasta was perfectly drawn, an exquisite pyramid: "[T]he regularity and symmetry of its outlines remain unrivaled. The mountain begins to leave the plain in slopes scarcely perceptible, measuring from two to three degrees. These are continued by exquisitely drawn gradations" to the surmounting crater (522).

Having painted the picture, he steps in through the frame with his climbing partner Jerome Fay. "For him," Cohen says about Muir, "it was not as important to view the scene as to be *in* it . . ." (241). Working with Fay to record "barometrical observations," his close inspection of the jagged cliffs and fumaroles of Mount Shasta is registered with the knowledge that the tourists to whom he writes will stay in the valley.

With his step inside the frame, the adventure story begins.

Fay and Muir make their climb three months before the regular climbing season begins and carry instruments designed to study fluctuations in weather. After two beautifully clear days, Muir and Fay are enveloped by a violent snowstorm. To give the reader an idea of the magnitude of the storm, Muir employs another conventional element of scenic description, the prospect view, which establishes "the larger spatial context in which . . . action takes place" (Nevius 30). As the heavy clouds begin to stir and brew, Muir looks about to see that:

> [t]he black lava beds made famous by the Modoc war; many a snow-laden peak far north in Oregon; the Scott and Trinity mountains; the blue Coast Range; Shasta Valley, dotted with volcanoes; the dark coniferous forests filling the valleys of the Upper Sacramento—were all in turn obscured, leaving our own lofty cone solitary in the sunshine, and contained between two skies—a sky of spotless blue above, a sky of clouds beneath. (Muir 526)

Here again are the contrasts essential to a picturesque scene: the clouds are absent from above, but obscure all below. And, as the snow falls, Muir records that it touched them "not a whit more harshly than warm rain on the grass" (528). Muir's experience on the mountain would be a sharp contrast to the experience of an ordinary tourist, safely within reach of shelter below, for he finds himself in a world where the trees are "crushed by winter snow, and shorn off by the icy winds," a world of "frost wind" and "scalding gas jets." Muir appears to address the absent readers as they sit comfortably fireside with their copy of *Harper's*:

> The ordinary sensations of cold give but faint conceptions of that which comes on after hard exercise, with want of food and sleep, combined with wetness in a high frost wind. (529)

To warm themselves, Muir and Fay find their way to a small patch of volcanic earth and are warmed by the thermal activity. The two explorers spend seventeen hours on this quarter acre of ground where contrasting temperatures pose dangers to their lives. From above they are threatened by the icy snowstorm; from below noxious fumes could poison them:

> The acrid incrustations sublimed from the escaping gases frequently gave way, opening new vents, over which we were scalded; and fearing that if at any time the wind should fall, carbonic acid, which usually forms so considerable a portion of the gaseous exhalations of volcanoes, might collect in sufficient quantities to cause sleep and death, I warned Jerome against forgetting himself for a single moment. . . . (528–29)

They suffer "the pains of a Scandinavian hell, at once frozen and burned" (Muir 529). It is a truly sublime experience, filled with terror, yet offering opportunities to reflect on life, death, and the infinite, which Muir and Fay (dutifully observing the conventions of sublimity) do. Fay wonders if prayers would help them, but Muir seems to dissuade him from praying with a rather deterministic speech about "the unflinching fair play of Nature." Violent tempests that threaten the lives of humans are all part of the Design: "Life is . . . a mere fire, that now smoulders, now brightens, showing how easily it may be quenched" (Muir 529).

Muir and Fay survive the night. "Snow-Storm on Mount Shasta" ends abruptly as they slide and shuffle into their camp, impeded by frozen trousers and hunger. Their descent is a descent from the sublime to the picturesque, both scenically and intellectually. For the sublime is the world of the Romantic and the Romantic's inward-turning eye; it inspires awe because it is too large to comprehend. But the picturesque can be appreciated by anyone who is familiar with painting; the picturesque is simple, flat, contained. When Muir returns to the chaparral zone he steps back through the picture frame. From the safety and comfort of his distant hotel room he may admire, for the audience, the view in the frame: the next morning "from the window I saw the great white Shasta cone wearing its clouds and forests, and holding them loftily in the sky" (Muir 530). In his assessment of Muir's life and work, Frederick Turner has noted that the cheerful ending gives no clue that Muir was suffering from severe frostbite (229).

"In the Heart of the California Alps," like "Snow-Storm on Mount Shasta," also places an adventure story within an artistic frame. Muir uses the elements of the picturesque and the sublime more self-consciously than in the earlier piece, often drawing attention to the qualities of nature that are similar to the elements of a painted landscape. For example, he sets his narrative in Indian summer and opens by "painting" the scene of the Tuolumne Valley with lavish detail:

> The intense azure of the sky, the purplish grays of the granite, the red and browns of dry meadows, and the translucent purple and crimson of huckleberry bogs; the flaming yellow of aspen groves, the silvery flashing of the streams, and the bright green and blue of the glacier lakes. (Muir 346)

The writing in this essay is less rough than "Snow-Storm on Mount Shasta," for Muir dispenses with diagrams and scientific pretenses and draws attention to the artistic qualities of the wilderness instead. He takes as his companions two artists in search of "a landscape suitable for a large painting" (Muir 346). Despite the fact that one of the artists (who remains nameless in the essay) was a close friend of Muir's named William Keith (Turner 209), it is clear from the text that the painters are constructed as possessors of picturesque eyes, interested only in what they can paint and not in the finer, less accessible, but more rewarding aspects of sublime experience.

Symbolically, Muir's ascent of Ritter represents a passage out of the banal appreciation of the picturesque to the greater understanding of the sublime. At times, however, Muir seems somewhat more sympathetic to the picturesque qualities of the valley, at one point remarking that the valley was waiting for "the elected artist"— "I could not help wishing that I were that artist," he laments (346). Nevertheless, although he is wont to throw up his arms "to inclose [the Tuolumne Valley] as in a frame" (346) and to wax eloquent on its majesty, it is significant that he eventually leaves the painters behind to sketch views while he alone accepts the challenge of climbing to the summit of Mount Ritter. Frederick Turner remarks, "as far as anyone knew it had never been climbed. Moreover, at this season (the last days of August), though the weather was still clear, there was the ever-present danger of snow. For Muir, all the conditions were right for climbing . . ." (209). Ritter posed a challenge for the individualist Muir.

At the start of the ascent to Mount Ritter, Muir notices that the best view of the California Alps comes from the headwaters of the Tuolumne River. Muir directs the reader's gaze to a scene he describes as "in a high degree picturesque, and in all its main features so regular and evenly balanced as almost to appear conventional" (345). He divides it into the traditional artistic foreground, middleground, and background. The foreground is the "magnificent valley" resplendent in autumn colors of brown, purple, and gold. It is "smooth, meadowy" and "level," dotted with "dipping willows and sedges" and "groves of arrowy pine." Through the foreground the waters of the Tuolumne flow from their source in the middleground, where it pours from "crystal fountains" and leaps in "white cascades." The middleground also contains the restricting "off-skips," narrowing and focusing the viewer's eyes toward the background. The off-skips in this painting are the "granite bosses" and the walls of the valley, "beveled away on both sides so as to embrace it all without admitting anything not strictly belonging to it." The background is colored in contrast to the foreground. The sky is cobalt blue, the glaciers are black, gray, and "pure, spiritual white." The focal point of this picture is "one somber cluster of snow-laden peaks . . . surging free into the sky" from the valley (345).

Curiously, while cataloguing the picturesque features of the scene from the valley, Muir asserts that "[f]ew portions of the California Alps are, strictly speaking, picturesque" (345). He argues that making a picture of these Alps would require separating the magnificence of the range to allow the discrete picturesque elements to be appreciated in isolation. However, he asserts, separating each mountain from the others so it might serve as the focal point of a painting would damage the incredible impression made by the whole range:

> The whole massive uplift of the range, four hundred and fifty miles long, by about seventy wide, is one grand picture, not clearly divisible into smaller ones; in this respect it differs greatly from the older and riper mountains of the Coast range. . . . But all were not brought forth simultaneously; and, in general, the younger the mountain landscapes, the less separable are they into artistic bits capable of being made into warm, sympathetic, lovable pictures. (345)

The artist companions, functioning as tourist-surrogates, are searching for such "artistic bits." Early in their journey into the mountains, they comment, "All this is sublime, but we see nothing as yet at all available for effective pictures" (Muir 346). Yet, although they are able to recognize the elements of the sublime, they are without feeling for it. The sublime does not create in them the appropriate response of fear and wonder. They are innocents, unable to wrestle with the implications of God in the wilderness. Their Puritan notion of the wilderness as something alien to humans, something to be conquered, gives root to their desire to tame the wild through pictorial representation—reducing it to a canvas three feet by four feet, imposing composition on the chaotic elements. The artists seek something recognizable, something known, something familiar, like the tourists on their approved path, following a conventional guidebook.

In the earlier article, Muir positioned himself in opposition to an assumed audience of tourists. He was able to find sublimity in a landscape where others found only views. It is evident in "In the California Alps" that Muir values the primacy of his *own* experience, and he hints that only he has the strength and the understanding to come to love the mountains, asserting that it is only after the mountains have been studied "one by one, long and lovingly," that one can begin to understand their full grandeur. Ironically, "loving" the mountains embodies the very aesthetic that he opposes—familiarizing the mountains into something to be framed and placed over a mantlepiece, destroying their ability to inspire fear and awe. In admitting his own attachment to the mountains, Muir deviates significantly from the conventional sublime response to the peaks—terror (Nicolson 356).

Loving, or "familiarizing," according to Walker Percy, is an inevitable part of being a tourist. Percy notes that visual, touristic, experience is bound by a "symbolic complex," a formulation of expectations prefigured by textual treatments (55). Satisfaction is measured by the way the tourist's experiences conform to the symbolic complex. So pervasive were the conventions of the picturesque in the nineteenth century (as John Sears in his work on nineteenth-century tourism and Nicolson have emphasized) that Muir's artist friends could not see beyond their expectations. They instead seek the familiar: a landscape suitable for painting. With the popular European Alps etching the scheme of mountains in their minds, Muir's artists eventually find a "landscape suitable for a large painting," and Muir records that one of the artists "dashed ahead, shouting and gesticulating and tossing his arms in the air like a madman. Here, at last, was a typical Alpine landscape" (346). With this incident, Muir not only points out to his readers that typical Alpine scenes are available for viewing in California, he shows the extent to which searching for the typical is ridiculous. So excited is this artist at finding a landscape which matches his conception of the European Alps, that he is blind to the authentic and particularly Californian charms of the Sierras. In this, as in other passages in these two essays, Muir invites readers to partake of the scenery while simultaneously drawing attention to the shortcomings of prefigured vision.

While the artists decide to remain at their mountain camp and sketch, Muir plans to continue climbing to the summit of Mount Ritter heretofore only visible as the focal point of the background, the "grand masterpiece." Again, as in "Snow-Storm on Mount Shasta," he steps through the foreground and middleground of the picture he paints. As he crosses the foreground, he traces "happy streams" to the "foot of a white cascade," which announces the beginning of the middleground, where he finds "painted meadows" and silvery lakes. When Muir begins to climb through the middleground toward his destination of the backdrop, he is able to look back on the land he has just traversed. It emerges as a prospect view, the far reaches of which exist in Muir's imagination:

> Over the summit, I saw the so-called Mono desert lying dreamily silent in thick, purple light—a desert of heavy sun-glare beheld from a desert of ice-burnished granite. Here the mountain waters divide, flowing east to vanish in the volcanic sands and dry sky of the Great Basin; west, to flow through the Golden Gate to the sea. (347)

As Muir pushes further toward the summit of Mount Ritter, he moves deeper into the realm of the sublime. The landscape now is full of "savage peaks," "spurs," and plunging "gorges"; it is sparse and bare. Such surroundings are the surroundings of the Romantic and Muir writes:

> In so wild and so beautiful a region my first day was spent, every sight and sound novel and inspiring, leading one far out of oneself, yet feeling and building a strict individuality. (347)

Although the picturesque is still evident here, in "little gardens" that decorate natural streams and pools, for instance, Muir is in the realm of the sublime. Sights and sounds are "novel." Like ruins atop hills, the flat-topped spurs are "marked and adorned with characteristic sculptures of the ancient glaciers that swept over this entire region like one vast ice-wind . . ." (347). When Muir sets his camp, he is encircled by "somber peaks, hacked and shattered . . . wearing a most savage aspect." A waterfall runs nearby, and "scraggy pines" in "rock-fissures" were "dwarfed and shorn" by wind (348).

Crossing mountains, Muir arrives at the final summit before that of Mount Ritter:

> There, immediately in front, loomed the majestic mass of Mount Ritter, with a glacier swooping down its face nearly to my feet, then curving westward and pouring its frozen flood into a dark blue lake, whose shores were bound with precipices of crystalline snow; while a deep chasm drawn between the divide and the glacier separated the massive picture from everything else. (349)

Although he is now amidst the sublime, the composition of the scene upon Muir's arrival atop the final summit before that of Mount Ritter is again a basic three-part structure recalling the picturesque. The foreground consists of the summit upon which he stands, the middleground is a grouping of a deep chasm, a glacier, and a lake toward the left side of the side-screen, and the background is the peak of Ritter itself. The atmosphere is far from placid and ordered, however. He faces steep gullies and vertical cliffs, which only emphasize the size of the mountain that lies ahead. Muir is atop an adjoining summit, so his view is not from the base of Mount Ritter, but from an elevation equal to about a third to half of Ritter. His vantage point does not come close to equalizing the relationship between his summit and the one that lies in front. Instead "massive battlements" stand forth, roughly hewn and shadowed. Even more telling, "huge, crumbling buttresses" extend to Muir's right and to his left, as far as he can see (Muir 349).

Suddenly, Muir's descriptions take on eery and unearthly overtones that seem to correspond to his reach into the sublime atmosphere that surrounds the summit of the mountain. Muir begins to employ bodily metaphors to emphasize the seemingly incomprehensible size of Mount Ritter, lying ahead; he defamiliarizes what had earlier been familiar, "loved," even understood. Turner recalls that Muir, traveling in his early years, had experienced a "dangerous weakness" from lack of bread (189), and perhaps the visions that he experiences here were induced by such deprivations. While the "head of the glacier sends up a few finger-like branches," Muir picks his way through numerous "narrow-throated gullies" and "across the yawning chasm," he hears the "gurgling of small rills down in the veins and crevasses," and he discovers "the mouth of a narrow avalanche gully." These human-like metaphors serve to reduce the extraordinary size and distance which he confronts, a technique employed, for example, by painter Thomas Cole in his *Snow Squall, Winter Landscape in the Catskills.* In a book that offers a psychoanalytical reading of American art history, Bryan Jay Wolf comments that the viewer will relate to the foreground plane of Cole's painting, a rocky promontory which juts vertically into a vacant chasm. A wolf and a few barren trees are the visible inhabitants of that promontory. However,

> [t]he wolf and trees that accommodate him, however uncomfortably, to the promontory world, individuating it and rendering it on human scale, either disappear in the middle-ground space or reappear in the case of the background forests in such proportions that their scale seems threatening and annihilating. . . . By traversing the valley and encountering the change of scale it implies, the viewer undergoes a process of "defamiliarization." The veil of familiarity is lifted from the face of nature and an alien strangeness left in its stead. (186)

Once looked upon "long and lovingly," the mountains are now something grotesque and fearsome, underscoring the deathly situation in which Muir soon finds himself: "at the foot of a sheer drop in the bed of the avalanche channel" (350). Although he clings to rocky footholds and handholds he fears that his doom is fixed. "I *must* fall. There would be a moment of bewilderment, and then a lifeless rumble down the one general precipice to the glacier below" (Muir 350). If, as Hussey sets forth, the mountains are "a *memento mori* on a gigantic scale" (Hussey 55), it is fitting that Muir should encounter imminent death clinging to the face of the most sublime of all peaks. It is significant, too, that his faith in the infinite once again allows him to survive:

> I seemed suddenly to become possessed of a new sense. The other self—the ghost of bygone experiences, Instinct, or Guardian Angel—call it what you will—came forward and

> assumed control. Then my trembling muscles became firm again, every rift and flaw in the rock was seen as through a microscope, and my limbs moved with a positiveness and precision with which I seemed to have nothing at all to do. Had I been borne aloft upon wings, my deliverance could not have been more complete. (Muir 350)

Above the place where Muir faces his destiny, he describes the mountain as a place "savagely hacked and torn," chasms "yawn," "detached bowlders [sic]" fill the "crags." Nevertheless, befitting the mystical aesthetic of the sublime, despite its potentially horrendous consequences, the peak and his experience there is "glorious," and Muir stands suffused in "blessed light" (350).

Following his harrowing experience, Muir descends toward the valley, returning to the realms where the familiar scenic conventions of the picturesque dominate. The landscape becomes more composed. Mountains arch into the background, their peaks "swelling higher, higher as they sweep on southward" (350). Natural ruins abound: Cathedral Peak is "a temple of marvelous architecture," a mountain seems a "gigantic castle with turret and battlement, the clusters of Alps are "eloquent monuments of the ancient ice-rivers that brought them into relief" (351).

Back at the camp, Muir finds the artists worrying over his safety. They feared that he had been overtaken by the elements, not knowing that it was he who triumphed over the elements. Muir comments that their troubles seemed "curious." After all, his journey had been "only a matter of endurance and ordinary mountain-craft," and he had been absent only three days when he had warned that he might be absent for over a week (Muir 352).

The artists pack "their precious sketches," concluding the "fine double excursion" of artists and scientist into the picturesque and the sublime.

Muir's uses of the conventions of picturesque and sublime description were an inevitable result of the literary climate in which he worked. Yet, as I mentioned earlier, there is also a strong subversive element in his writing. Literary critic Marvin Fisher asserts that Muir's contemporary Herman Melville was a subversive writer, forced to "go underground" in order to satirize the very audience for whom he wrote. These two essays, when examined in light of Muir's own comments elsewhere and revelations of his predispositions by his biographers, seem to indicate that Muir too sought to satirize and patronize an audience upon whom he depended for financial support. Muir found himself linked to an audience for whom he held little respect. Fearful of the encroachments of technology, he was fighting to preserve the wilderness of the American West. He realized that his stories of the mountains would raise public awareness of western beauty and would be instrumental in enjoining Americans to protect the wild regions of Yosemite from farming and industry. Cohen points out that "Americans would need some encouragement, would need to know not only what they possessed, but why it was worth protecting and how this could be done" (205). Because the literary conventions of the sublime and the picturesque were well worn and would be well recognized by his readers, their effect was to make an unfamiliar landscape familiar to readers living thousands of miles away, something politically necessary.

Muir's texts are problematic, revealing a narrator in conflict about his role as preservationist and writer, for he knew his stories would extend beyond the page to encourage tourism, and he worried that the pristine land would be overrun by tourists in search of the picturesque. In his biography of Muir, Cohen notes that it was difficult for Muir to hide his contempt of complacent tourists, eager only for a view and not for knowledge about their surroundings (129, 207). To illustrate his point, Cohen draws from this letter written by Muir to his friend Jeanne Carr. Muir wrote, "They climb sprawlingly to their saddles like overgrown frogs pulling themselves up a stream bank through the bent sedges, ride up the Valley with about as much emotion as the horses they ride upon—are comfortable when they have 'done it all' and long for the safety and flatness of their proper homes" (Bade 220). His attitude toward the leisured class takes on importance in a study of his style, for it seems ironic that one so vehemently opposed to the domestication of the wild would seek not only to entice visitors forward, but would, though his very language, reduce Nature into a series of "fine scenes" for the pleasure of the audience.

Yet Muir was prepared to pander to the "frogs," and he did so at least in part through his application of the conventions of picturesque description. In his verbal landscapes, mountains become frosty cones settling into backdrops; sparkling lakes and twisted trees dapple his foregrounds. And it is quite surprising that Muir often pauses in his narration to point out "views." Coupled with his own stories of adventure and extreme exposure to inhospitable elements, the views seem inconsequential, almost afterthoughts. At times, especially after the more harrowing of Muir's adventures, his references to fine scenes seem a harshly reductive view of nature. Like the artists who accompany him on his journey into the heart of the California Alps, Muir loved mountains. His prose made them accessible, beautiful, and orderly, rather than terrifying and forbidding. In many ways, through his writing, Muir destroyed the aspects of the mountains that he prized most: their seclusion, their remoteness from human intervention, their inhospitability. Described according to traditional artistic and literary conventions, the Sierras lost their uniqueness, becoming just another typical example of an aesthetic norm determined by the European Alps.

When the artists with whom he travels into the California Alps pack their sketches, they close the book on nature. Muir, however, distinguishes himself as a privileged observer by finding the book continuously open. He would return to read "the records she has carved on the rocks, reconstruct . . . the landscapes of the past" (Alps 351). While Muir textually domesticated nature, reducing it into a series of fine scenes for an appreciative audience, he preferred to leave the reality wild, a setting for his many returns to the summits and peaks.

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***Marguerite Helmers** is Assistant Professor of English at the University of Wisconsin Oshkosh.*

Robin E. Jung

Blanchard's cricket frogs (Acris crepitans blanchardi) *in southwest Wisconsin*

Abstract *State-endangered Blanchard's cricket frogs* (Acris crepitans blanchardi) *were censused in southwest Wisconsin and found at 19 of 40 sites which historically were known or were thought to have had populations of this species. Blanchard's cricket frogs were found most often at sites with mud and vegetation banks and shallow slopes leading to the water, although these trends were not statistically significant (P > 0.15). Neither habitat variables (e.g., water depth, bank type) nor indices of water quality (pH, conductivity, oxidation-reduction potential, turbidity) differed significantly between sites with and without Blanchard's cricket frogs. However, water temperature was significantly greater at sites with cricket frogs than without (P = 0.011). The total number of frog and toad species at a site (range = 0–7) was positively correlated with water temperature (P = 0.017) and negatively correlated with turbidity (P = 0.021). In addition, significantly more anuran species were found at sites without agricultural fields nearby (P = 0.0026).*

Recent reports of declining amphibian populations around the world (Blaustein and Wake 1990; Lohmeier 1990; but see Pechmann et al. 1991) have instigated research efforts toward understanding potential causes (e.g., habitat loss, pesticides, acid rain, drought). In Wisconsin, the Blanchard's cricket frog (*Acris crepitans blanchardi*) has declined precipitously during the last two decades (Vogt 1981; Mossman and Hine 1985) and has been on the State Endangered list since 1982 (Bureau of Endangered Resources 1989). Habitat loss, drought, and polluted water are a few of the factors hypothesized to have caused Blanchard's cricket frog population declines (Minton 1972; Oldham 1992; L. A. Wilsmann, pers. comm.). Wisconsin represents the northern limit of the geographic range of Blanchard's cricket frogs (Conant and Collins 1991), and it is possible that routine physiological stresses (e.g., during overwintering; cf. Bradford 1983) may be relatively high. Thus, Wisconsin populations of this species might be particularly sensitive to additional stressors, such as those related to deteriorating water quality.

M. J. Mossman and R. L. Hine (Mossman and Hine 1984, 1985) of the Wisconsin Department of Natural Resources (WDNR) initiated the Wisconsin Frog and Toad Survey in 1981. Relatively few (2 of 63) of the early WDNR survey routes, however, were located in southwest Wisconsin (Grant, Iowa, and Lafayette counties), where Blanchard's cricket frogs still occur (Mossman and Hine 1985).

The purpose of this study was to survey Blanchard's cricket frogs in southwest Wisconsin, and to determine whether selected habitat and water quality variables were related to the presence or absence of Blanchard's cricket frogs or other frog and toad species.

Methods

During the summer of 1991, I conducted a census of the Blanchard's cricket frog in southwest Wisconsin (Dane, Grant, Iowa, and Lafayette counties). I chose to study 40 sites which, according to records provided by the WDNR (Wisconsin Natural Heritage Inventory Program; Wisconsin Frog and Toad Survey, M. J. Mossman, pers. comm.) and the Milwaukee Public Museum (Wisconsin Herpetological Atlas Project, G. S. Casper, in prep.), were historically reported to support Blanchard's cricket frog populations. The sites were visited an average of 2.6 ± 0.99 times (range = 1–4) between 11 May and 17 July, during the peak chorusing season for cricket frogs (Vogt 1981). Most sites were visited at least once during the day and once at night. If no chorusing was heard, a tape recording ("Wisconsin frogs," produced by R. Anderson and D. Jansen, University of Wisconsin–Stevens Point) of Blanchard's cricket frog vocalizations, which is thought to elicit chorusing, was played for two minutes (Mossman and Hine 1985). Frogs and toads were identified by call, sight, and/or catching animals by hand. Numbers of calling males were estimated by walking the water's edge, noting differences in directions of calls, and listening for distinct vocalizations. Spring peepers (*Hyla crucifer crucifer*), western chorus frogs (*Pseudacris triseriata triseriata*), northern leopard frogs (*Rana pipiens pipiens*) and pickerel frogs (*Rana palustris*) were not adequately censused as they chorus primarily from March to May (Vogt 1981). Seven of the sites I censused were also covered in 1991 by the Wisconsin Frog and Toad Survey, so I incorporated additional species-presence data from this source as well.

Water samples were taken approximately 0.5 m from the water's edge. Four indices of water quality (temperature, pH, conductivity, oxidation-reduction potential [ORP]) were measured using a Cole-Parmer Water Test, Model 05556-00. Conductivity represents the total concentration of electrolytes in solution (higher conductivities corresponding to higher ion content, particularly Ca^{++}, Mg^{++}, Na^{+}, and K^{+}) and is expressed in micro-Siemens (Wetzel 1983). ORP, measured in millivolts (mV), is proportional to the equivalent free energy change per mole of electrons associated with a given reduction. Large, positive ORP values signify strongly oxidizing waters. In addition, turbidity of a water sample in a beaker was estimated by eye and scored on a scale of 0–5, ranging from clear to muddy.

Habitat variables assessed included: (a) whether the site was a lake/pond or stream/river, (b) water depth 10 cm from the edge, (c) percent cover of water area by rooted aquatic plants, (d) percent cover of water area by algae, (e) composition of water bottom (mud, mud and rock), (f) bank type (mud, mud and vegetation, vegetation), (g) bank slope (flat, flat and steep, steep), and (h) whether the site was adjacent to pasture land (primarily with cows) and/or agricultural land.

All statistical analyses were performed using SPSS (Norusis 1988). Significance was judged at $P < 0.05$. Yates' correction was used for chi-square tests of independence when any expected frequencies were < 5. For water quality analyses, I used mean values for pH, water temperature, conductivity, and ORP; I also computed a mean visitation date for each site to use as a covariate in statistical analyses.

Results

Habitat data for 39 sites (excluding Iowa County site 16) are presented in Table 1. No habitat data were collected for Iowa County site 16 because the lake had been completely drained in the spring of 1991, and Blanchard's cricket frogs no longer occurred there. Site locations are not presented here (see Wisconsin State Statute 23.27, section 3, paragraph B; Casper 1989), but are available from the WDNR Natural Heritage Inventory Program upon request. Blanchard's cricket frogs were found at 19 of the 40 (48%) sites which historically were reported to have supported cricket frogs. I estimated 125 cricket frog calling males at 18 sites (Table 1). Assuming equal sex ratios (see Pyburn 1958), the population estimate (males and females) for these sites is 250 frogs, yielding a mean ± standard deviation (SD) of 14 ± 9.6 frogs per site.

Blanchard's cricket frogs were heard chorusing during the day (between 11 a.m. and 6 p.m.) on seven occasions, but were most often heard chorusing after 6 p.m. (18 occasions). Breeding choruses of the Blanchard's cricket frogs tended to be dense (males within one meter of each other) and localized in mudflat areas or in vegetated shallow water habitat (see Perrill and Shepherd 1989). Exact densities of frogs or inter-male spacing were not recorded in order to avoid disturbing frogs and habitat and also because of the difficulty in delineating how much area comprised suitable habitat.

Chi-square and Mann-Whitney U tests indicated that the presence of Blanchard's cricket frogs was not related to the habitat variables I recorded. Of the 19 sites where Blanchard's cricket frogs were present, 12 were categorized as stream/river habitats and seven as pond/lake sites; cricket frogs were no longer present at 15 stream/river sites and 6 pond/lake sites ($X^2 = 0.311$, d.f. = 1, $P = 0.577$).

Most Blanchard's cricket frog populations were found at sites with flat slopes leading to the water's edge (17 of 19) and mud and vegetation banks (17 of 19; all with mudflats). However, because most sites surveyed had flat slopes (34 of 39) as well as mud and vegetation banks (30 of 39), the distribution of Blanchard's cricket frogs did not differ from random with respect to these habitat variables (X^2: $P = 0.614$ and 0.150, respectively). Only 6 of the 19 sites with Blanchard's cricket frogs were adjacent to agricultural (primarily corn) fields, yet a chi-square test comparing presence and absence of cricket frogs at sites adjacent versus not adjacent to agricultural fields was not significant ($X^2 = 1.766$, d.f. = 1, $P = 0.184$). No relationships were found between the presence versus absence of Blanchard's cricket frogs and pasture land, bottom type, water depth, or percent cover of algae or rooted aquatic plants. In summary, with respect to the variables measured, Blanchard's cricket

Table 1. Data for 39 sites in southwest Wisconsin.
Key: BC = Blanchard's cricket frog (0 = absent, 1 = present); #BC = estimated # of BC frogs; S = # of anuran species; H = Habitat (0 = stream/river; 1 = lake/pond); WD = Water Depth (cm); T = water temperature (C); C = conductivity (uS); ORP = oxidation-reduction potential (mV); Tu = Turbidity (0–5, clear-muddy); Aq = % rooted aquatic plants; Al = % algae; Bc (bottom composition): 1 = mud, 2 = mud/rock; Bt (bank type): 1 = mud, 2 = mud/vegetation, 3 = vegetation; Sl (slope): 1 = flat, 2 = flat/steep, 3 = steep; Cow: 0 = absent, 1 = present; Cr: 0 = no agricultural fields nearby, 1 = fields nearby. -9 indicates missing data.

Site	*BC*	*#BC*	*S*	*H*	*WD*	*pH*	*T*	*C*	*ORP*	*Tu*	*Aq*	*Al*	*Bc*	*Bt*	*Sl*	*Cow*	*Cr*
Dane																	
1	0	0	3	1	23	6.8	23.5	319	180	4	3	3	1	3	1	0	0
Lafayette																	
1	0	0	0	0	2	7.6	21.3	738	113	2	1	0	1	2	1	1	1
2	0	0	1	1	2	7.4	29.5	202	164	5	1	0	1	1	1	0	1
3	1	7	2	0	10	7.7	24.1	863	164	3	1	0	2	2	1	1	0
4	0	0	1	0	13	7.3	23.4	799	191	0	1	1	2	1	1	1	1
Iowa																	
1	1	10	5	0	10	8.1	24.6	571	152	2	1	1	1	2	2	1	1
2	1	7	3	0	10	8.6	28.7	306	126	0	2	1	1	2	1	1	0
3	1	20	4	1	10	8.6	27.1	191	113	0	1	2	1	2	1	1	0
4	1	-9	6	1	6	8.5	30.8	394	122	-9	1	1	1	3	1	0	0
5	1	1	3	1	-9	8.8	30.6	426	145	-9	1	1	1	2	2	0	0
6	1	3	7	1	22	8.0	29.2	511	111	-9	1	3	1	3	1	0	0
7	0	0	6	1	10	8.2	33.4	443	95	0	-9	3	1	2	1	0	0
8	0	0	1	1	-9	8.4	28.1	408	52	-9	1	2	1	2	1	0	0
9	1	3	3	0	5	7.6	25.1	663	152	0	1	1	2	2	1	0	0
10	1	10	4	1	10	8.4	32.1	472	163	-9	1	1	1	2	1	0	0
11	1	10	6	1	4	7.9	25.8	483	151	0	1	1	1	2	1	0	0
12	0	0	0	1	20	7.9	19.3	468	144	1	1	1	2	3	2	1	1
13	0	0	2	0	20	8.1	20.8	463	139	0	1	1	1	2	1	0	0
14	0	0	0	0	3	7.7	19.0	467	169	2	1	1	2	3	3	0	1
15	0	0	0	0	6	7.8	23.5	577	144	2	1	1	1	2	1	0	0
Grant																	
1	1	2	3	0	6	7.6	23.1	738	132	0	1	1	2	2	1	0	0
2	1	2	3	0	5	8.0	24.9	728	152	1	1	1	1	2	1	1	0
3	1	4	2	0	6	8.2	27.7	834	124	1	1	1	2	2	1	1	1
4	1	10	1	0	6	8.1	25.3	769	131	2	1	1	2	2	1	1	1
5	1	9	3	0	4	8.3	25.0	519	133	2	1	1	2	2	1	0	1
6	0	0	1	0	6	8.0	23.7	751	117	1	1	1	2	2	1	1	0
7	0	0	2	0	15	7.5	15.3	719	41	3	1	1	2	2	1	1	0
8	0	0	2	0	6	7.8	18.5	754	151	0	1	1	2	2	1	0	0
9	1	6	2	0	9	7.3	30.7	705	118	0	1	3	1	2	1	1	1
10	0	0	1	0	15	8.0	24.9	672	151	3	1	1	1	2	1	1	1
11	1	1	1	0	3	7.3	32.4	805	75	3	1	3	1	2	1	0	0
12	0	0	2	1	2	8.7	29.5	518	121	0	1	1	1	2	1	0	0
13	0	0	2	0	5	8.1	25.1	573	158	2	1	1	1	3	2	1	1
14	0	0	0	0	3	8.3	26.4	615	154	0	1	1	1	2	1	0	1
15	0	0	2	0	10	7.9	24.3	577	171	1	1	1	1	3	1	1	1
16	0	0	1	0	8	8.1	26.3	582	165	1	1	1	1	2	1	1	1
17	0	0	2	0	20	8.1	24.7	608	163	1	1	1	1	2	1	0	1
18	1	10	2	0	3	8.3	25.7	565	153	0	1	1	2	2	1	1	1
19	1	10	5	0	4	7.9	24.2	727	119	0	1	1	2	2	1	1	0

frogs had disappeared from sites whose habitat characteristics were similar to sites where they still occurred.

Using t-tests (Mann-Whitney U tests for turbidity), only one water quality variable, temperature, differed significantly between sites with and without Blanchard's cricket frogs ($t = 2.68$, d.f. = 37, $P = 0.011$). The mean (± SD) water temperature for sites with Blanchard's cricket frog was 27.22 C (± 2.971), as compared to 24.03 C (± 4.297) for sites without cricket frogs. Because water quality variables may vary with date, I also performed analyses of covariance predicting water quality variables with date and presence/absence of cricket frogs (scored as a 0–1 dummy variable). Both date ($F = 4.991$, $P = 0.032$) and presence/absence of cricket frogs ($F = 6.571$, $P = 0.015$) were significant predictors of temperature. However, presence/absence of cricket frogs was not a significant predictor of pH (mean range = 6.8–8.8), conductivity (mean range = 191–863), ORP (mean range = 41–191), or turbidity.

Blanchard's cricket frogs were found most often with green frogs (*Rana clamitans melanota*; 15 of 19 sites = 79%) and to a lesser extent with eastern gray tree frogs (*Hyla versicolor*) and American toads (*Bufo americanus*) (63% and 53%, respectively). Green frogs occurred most frequently, recorded in 29 of the 39 sites.

Thirty-four of the 39 sites (87%) supported anuran populations (Table 2). The greatest number of species recorded at any one site was seven (including data from the Wisconsin Frog and Toad Survey). To determine whether the number of species present at a site was related to the categorical habitat variables, I categorized sites as having either few (0–2) or many (3–7) species. Eight of 12 pond/lake sites had many species, whereas 21 of 27 stream/river sites had few species ($X^2 = 5.33$, d.f. = 1, $P = 0.021$). Also, 13 of 22 sites situated away from agricultural fields had many species, whereas 15 of 17 sites adjacent to agricultural fields had few species ($X^2 = 9.07$, d.f. = 1, $P = 0.0026$).

Species richness showed a significant positive correlation with water temperature (Pearson's $r = 0.381$, $n = 39$, $P = 0.017$) and a negative correlation with turbidity (Spearman's $r = -0.395$, $n = 34$, $P = 0.021$) (Table 3). In a multiple regression analysis, only temperature was a significant predictor of species richness. pH was significantly positively correlated with temperature, and negatively correlated with both conductivity and turbidity (Table 3).

Discussion

My estimates of Blanchard's cricket frog populations at each site are extremely conservative, because I did not attempt to capture all frogs, and frogs may not have been chorusing during visits. Even if frogs were chorusing, I may have underestimated the number of males since some males assume noncalling, or satellite, positions (see Perrill and Magier 1988). The sampling method I used represents only the greatest number of calling males heard at a site during short visits, and therefore is tenuous. Indeed, at two sites in Iowa County (sites 2 and 3) where I could distinguish only 27 male Blanchard's cricket frogs, D. Nicolai (Mossman and Hine 1985) counted over 220 frogs in the early 1980s. This situation may very well be the case at the other sites, a fact that points to the need for intensive censusing (e.g., mark-recapture) efforts and long-term monitoring if reliable population estimates are to be obtained.

Previous studies indicate that Blanchard's cricket frogs prefer to breed in permanent

Table 2. Anuran species at 39 sites in Dane, Grant, Iowa, and Lafayette Counties. SP = spring peeper, CGTF = Cope's gray tree frog, CF = chorus frog, GF = green frog, BCF = Blanchard's cricket frog, EGTF = eastern gray tree frog, AT = American toad, LF = leopard frog, PF = pickerel frog. (X) = data from Wisconsin Frog and Toad Survey (WFTS, 1991, B. Dhuel, pers. comm.).

County Site	*SP*	*CGTF*	*CF*	*GF*	*BCF*	*EGTF*	*AT*	*LF*	*PF*
Dane									
1			(X)	(X)					
Lafayette									
1									
2						X			
3					X		X		
4				X					
Iowa									
1	(X)			X	X	(X)	X		(X)
2				X	X		X		
3				X	X	X	X		
4	(X)			X	(X)	X	(X)		(X)
5					X	X	X		
6	(X)	(X)		X	X	X	X		(X)
7	(X)			X		X			(X)
8				X					
9				X	X	X			
10	(X)		(X)	X	X	(X)	X	X	
11	(X)		(X)	X	X	X	X		X
12									
13				X		X			
14									
15									
Grant									
1				X	X	X			
2				X	X	X			
3				X	X				
4					X				
5				X	X	X			
6				X					
7				X		X			
8				X		X			
9				X	X				
10				X					
11					X				
12				X				X	
13				X		X			
14									
15				X			X		
16				X					
17				X		X			
18				X	X				
19				X	X	X	X		X

Table 3. Pearson product-moment correlation coefficients (Spearman rank order correlation coefficients for turbidity) for water quality variables in relation to number of anuran species (top line, with P values below, n = 39 except n = 34 for turbidity correlations).

	pH	*Temperature*	*Conductivity*	*ORP*	*Turbidity*
# of Anuran species	0.289	0.381*	-0.241	-0.048	-0.395*
	0.075	0.017	0.139	0.773	0.021
pH		0.360*	-0.329*	-0.138	-0.360*
		0.024	0.041	0.403	0.036
Temperature			-0.289	-0.127	-0.170
			0.075	0.442	0.338
Conductivity				-0.050	0.078
				0.762	0.662
ORP					0.163
					0.358

* Pairwise 2-tailed P < 0.05.

or semipermanent bodies of water (Pyburn 1958) with mudflats, shallow slopes toward the water, and mud and vegetation banks (Burkett 1984; Minton 1972). Most of the 40 sites studied, all of which were reported to have had cricket frogs at one time, fit this description.

Only one of the sites used by cricket frogs in the past had been destroyed (drained). However, this does not preclude the possibility that subtle site modifications (such as aquatic vegetational changes) in the past may have impacted cricket frog populations.

Blanchard's cricket frogs were present at sites with higher water temperatures compared to sites without cricket frogs, and number of amphibian species was positively correlated with water temperature. Sites with higher water temperatures may be preferred by anurans for breeding. On the other hand, anurans may simply be more likely to be observed on warm days. However, I do not think this could account entirely for the relationships with temperature, in part because most sites were visited more than once.

No sites contained pH levels considered toxic to aquatic organisms (pH < 4.5 or > 9.5; Wetzel 1983), and I found no correlation between species richness and pH. Conductivity was within the range considered normal for bicarbonate-dominated lakes and streams (Wetzel 1983), but did show considerable variability among sites (coefficient of variation, CV = 30%). Oxidation-reduction potential (ORP) also varied (CV = 23%), but the mean value for all sites was 136 ± 31.9 mV, which is substantially lower than 500 mV, a value expected for neutral, fully oxygenated water equilibrated with air (Wetzel 1983). Turbidity was lower at sites with more species, which may indicate preference for clearer waters.

Significantly fewer anuran species were found at sites near corn and other crop fields. This result suggests that fertilizer or pesticide run-off from agricultural fields may affect anuran populations. Herbicides and insecticides still used on corn in Wisconsin (Doersch et al. 1991) can be toxic to amphibians and may have a significantly negative impact on amphibian populations or their prey base (atrazine, Hazelwood 1970; Birge et al. 1980; malathion, paraquat, and toxaphene, Sanders 1970; Hall and Kolbe 1980; Linder et al. 1990). Hylids in general, such as cricket frogs, may be more susceptible to pesticides than other anuran species, such as toads (Sanders 1970; Birge et al. 1979).

Other factors which may adversely affect anurans in southwest Wisconsin are low dissolved oxygen and high nitrogen concentrations. On the Little Platte River in southwest Wisconsin, Holmstrom et al. (1988) reported dissolved oxygen concentrations as low as 3.1 mg/l in early July, which is below the recommended 5 mg/l dissolved O_2 concentration for housing amphibians (National Academy of Sciences 1974). As well, nitrate/nitrite and ammonia levels were as high as 5.1 mg/l and 1.6 mg/l, respectively, during the amphibian breeding season, which exceed the 0.3 mg/l nitrate/nitrite and 0.2 mg/l ammonia concentrations considered safe for amphibians in the laboratory (National Academy of Sciences 1974). On the other hand, three of the sites included in the present study were on the Little Platte River, and all still had Blanchard's cricket frogs.

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***Robin E. Jung** received her M.S. in Zoology in 1990 from the University of Wisconsin-Madison, based on studies of individual variation in fruit choice by American robins (*The Auk *109:98–111). She is currently working toward her Ph.D. in the Department of Zoology, studying amphibian ecotoxicolgy.*

Richard A. Lillie, Robert Last, Paul Garrison,
Paul Rasmussen, and John W. Mason

A survey of the summer phytoplankton communities of 579 Wisconsin lakes

Abstract *Phytoplankton and associated limnological data were collected from surface waters of a randomly stratified set of 579 Wisconsin lakes during the summer of 1979. Frequency of occurrence and relative dominance of phytoplankton genera were determined from preserved samples.*

Blue-greens were the most common and most frequently dominant taxa under all bloom conditions independent of sampling date (early to late summer). The frequency of occurrence of blue-green dominance increased with bloom severity (chlorophyll a *concentration). Blooms (defined as chlorophyll* a *concentrations above 10 µg/L) occurred above a threshold of 20 µg/L total phosphorus. Less than 7% of lakes that appeared blue or clear had any form of a bloom, while all lakes with severe or moderately severe blooms appeared either green, brown, or turbid. Quantitative definitions are presented for classifying the severity of phytoplankton blooms in Wisconsin lakes based on relationships between chlorophyll a and perceived water color.*

Phytoplankton blooms cause taste and odor problems in public water supplies and occasionally produce toxins that may be harmful to humans or livestock (MacKenthun et al. 1945; Rohlich and Sarles 1949; Gorham 1965; Gilbert 1990). Blooms are often comprised of algal species that are inedible, unpalatable, or toxic to zooplankton, thus affecting zooplankton standing crop, productivity, or community size-structure. Zooplankton, which utilize phytoplankton as a major food source, are, in turn, important food resources for fish. Therefore, phytoplankton blooms may seriously interfere with the efficient flow of nutrients and energy through the food chain. Nighttime respiration or the sudden death and collapse of blooms may cause total depletion of oxygen in the water column, resulting in fish kills (Mackenthun et al. 1945, Barcia 1975). In addition to these biological responses, the changes in water color that accompany the onset of a bloom (Lillie and

Mason 1983) may directly influence lake recreational use and affect lakeshore property values.

Direct control of phytoplankton blooms in Wisconsin has been primarily limited to the application of algicides containing copper. Many thousands of tons of copper sulfate have been applied to Wisconsin lakes since the early 1900s (Lueschow 1972). Over 20 tons of copper sulfate were applied to Lake Monona at Madison during 1935 alone (Domogolla 1935). The relative inefficiency of copper sulfate in controlling pelagic algae combined with environmental concerns of copper toxicity has led the Wisconsin Department of Natural Resources to ban whole-lake algae treatments (WDNR 1989) and has encouraged research and development of alternative management strategies to control blooms, including predator-prey manipulations and nutrient reduction.

Blue-green algae have long been recognized as being a dominant component of summer phytoplankton blooms in eutrophic lakes (Reynolds and Walsby 1975; Wetzel 1975; Spodniewska 1986; Stewart and Wetzel 1986; Canfield et al. 1989 among many others). Numerous phytoplankton studies (Sloey and Blum 1972; Bartell et al. 1978; Fallon and Brock 1980; Barko et al. 1984; Engel 1985; Narf 1985; Lathrop 1988; Barko et al. 1990; Klemer and Barko 1991) and general taxonomic surveys (Smith 1920; Smith 1924; Lackey 1945; Prescott 1970; USEPA 1978) of Wisconsin lakes and reservoirs indicate the important contribution of blue-greens to blooms in Wisconsin. However, because much of the previous work done in Wisconsin was restricted to eutrophic bodies of water, there was some concern that our perception of the problem may be wrong. Indeed, not all blooms consist of blue-greens; diatoms, dinoflagellates, and green algae were occasionally listed as dominant in some of the aforementioned studies. Consequently, in order to obtain a more accurate assessment of the composition of blooms on a statewide basis, we examined phytoplankton from a set of samples that had been collected in the summer of 1979 by the WDNR during an extensive limnological survey of 661 randomly selected Wisconsin lakes (Lillie and Mason 1983). Study objectives were (1) to determine the structural composition (occurrence and dominance) of summer phytoplankton communities in Wisconsin lakes, (2) to establish the relationship between bloom severity and composition of phytoplankton communities, and (3) to document the limnological characteristics of lakes experiencing blooms. Furthermore, because the lakes involved in this study were sampled only once during the summer, there was a legitimate concern that normal seasonal phytoplankton succession (per Stewart and Wetzel 1986; Bartell et al. 1978; Dokulil and Skolaut 1991) could invalidate our conclusions regarding dominance during blooms (i.e. the composition of blooms in lakes sampled early in the summer may have differed from blooms in lakes sampled later in the summer). Therefore, we evaluated the relationships between phytoplankton dominance and bloom severity between lakes sampled early in the summer versus lakes sampled late in the summer. This paper summarizes the conditions found during the summer 1979 survey and discusses the significance of these findings to lake management.

Study Sites

A stratified random sub-sample was selected from the approximately 2800 Wisconsin lakes over 10 ha (25 acres) in size and greater than 1.5 m (5 feet) deep. Lakes were stratified according to geographic distribution;

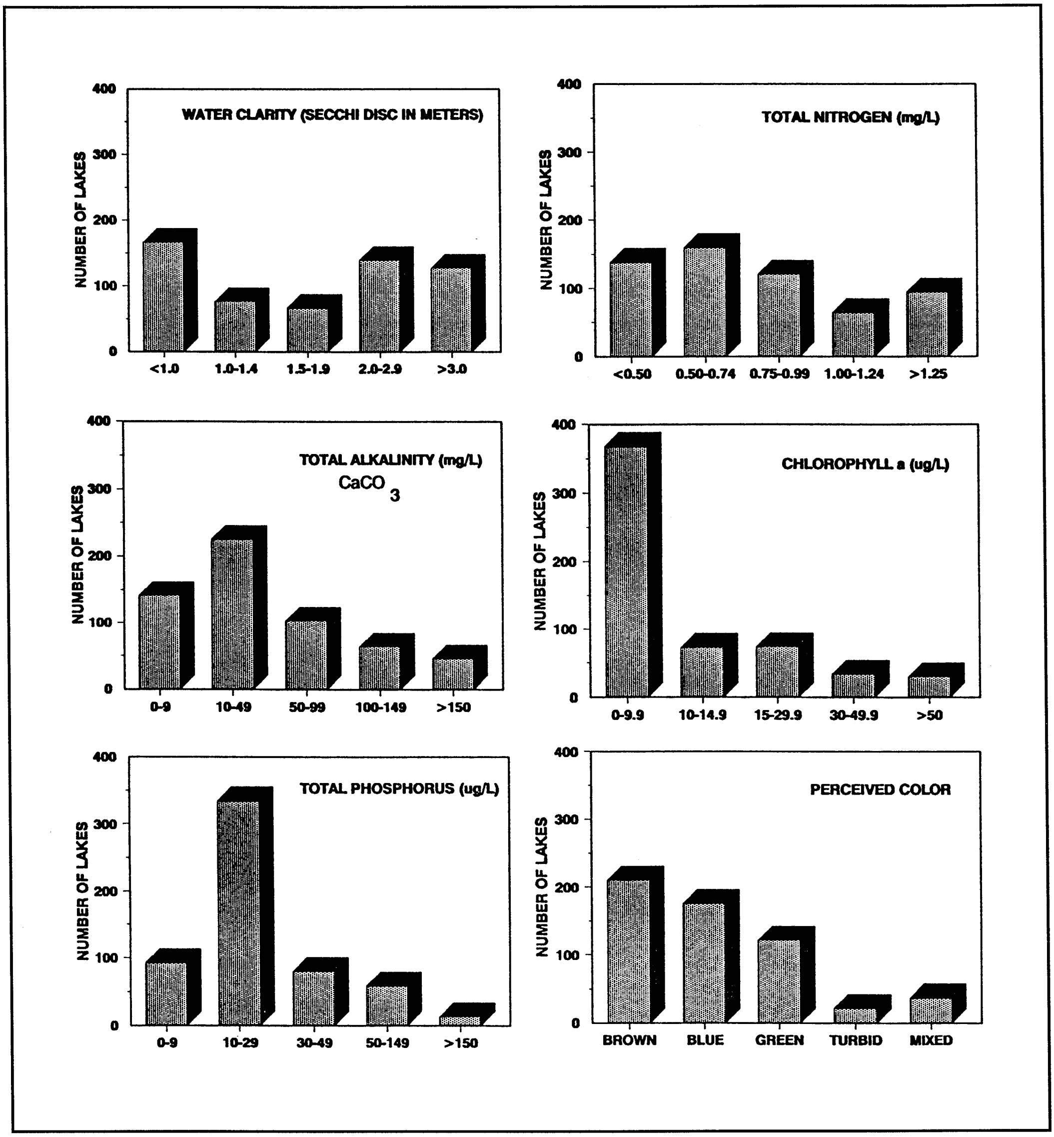

Fig. 1. Distribution of sampled lakes (N = 579) by water clarity (Secchi disc), total alkalinity, and total phosphorus, total nitrogen, and chlorophyll *a* concentrations, and perceived water color classification.

25% of all lakes present in each county were randomly chosen. Phytoplankton samples were available from only 579 of the 661 lakes in the survey. The sampled lakes represented a broad range of morphometric conditions and chemical compositions; sampled lakes were nearly equally divided between seepage (291) and drainage (287) and between thermally stratified (262) and mixed (256). Only 98 lakes were impoundments. Most lakes generally had low nutrient (nitrogen and phosphorus) and chlorophyll *a* concentrations and good water clarity (Fig. 1). Less than one third of the lakes were described as blue or clear. A more complete description of the limnological characteristics of the lakes in this study is provided in Lillie and Mason (1983).

Methods

One sample was collected from each of the 579 lakes during the period 7 July – 7 September, 1979. Samples were collected from the lake surface above the point of maximum depth (where known) or from a central basin location. All samples were preserved immediately in Lugol's solution. Aliquots were settled using the Utermohl settling technique (Lund et al. 1958) for a minimum of 4 hrs per cm settling tube height and analyzed at 1400 X and 560 X magnification using a Wild inverted microscope. Taxa identifications (to genus and species) were based on keys and descriptions provided in Smith (1920, 1924, 1950), Prescott (1970), and Weber (1971).

Dominance in algal communities may be computed on the basis of numerical abundance, biomass, or biovolume. Because cell sizes and chlorophyll content differ greatly among the various phytoplankton species, numerical dominance has less ecological significance than dominance based on either biomass or biovolume. Because biomass was not measured in this study, dominance of phytoplankton communities was based on estimates of relative biovolume. We developed and applied a semi-quantitative approach to evaluate cell biovolume dominance because quantitative determinations of cell biovolume of all 579 phytoplankton samples were economically impractical. Assessment of phytoplankton dominance was based on visual comparisons of cell biovolumes in scans of 40 randomly selected fields of view. Ratings of relative dominance and their respective numerical weights were defined as follows (see Fig. 2): absent (0) = not found; rare (1) = occurring in less than 5 fields, or if occurring in more than 5 fields then never accounting for more than 10 percent of the total biovolume in a field; present (3) = occurring in more than 5 fields but less than 10 fields and generally comprising 10–25 percent of the total biovolume in a field; important (5) = occurring in more than 10 fields and generally comprising 10–25 percent of the total biovolume in a field (but always secondary in rank to other taxa); codominant (7) = occurring in more than 5 fields and generally representing more than 25 percent of the total biovolume in a field but sharing dominance with one or more other taxa; and dominant (9) = occurring in more than 5 fields and representing more than 25 percent of the total biovolume and clearly dominant over other taxa. Samples in

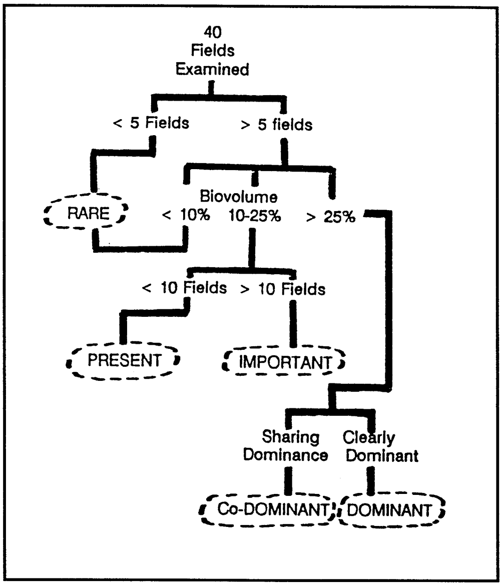

Fig. 2. Flow chart describing criteria for assessing phytoplankton dominance in visual scans of 40 randomly selected fields of view. Percentages (%)s refer to typical percent of total biovolume in most fields of view.

which dominance could not be clearly determined were identified as mixed assemblages. Numerical weights (numbers given in parentheses above) were averaged for all lakes (statewide) and separately for only those lakes in which the taxon occurred in determining the relative importance of each genus.

The accuracy of this method of assessing phytoplankton dominance was evaluated on a subset of lakes prior to applying the method to the entire set of samples. Independent assessments of cell biovolume dominance (by genus and class) were made by four limnologists (with a combined 30 years of experience) on a subset of 20 lakes selected to represent a broad range of phytoplankton communities. The 20 sets of assessments of phytoplankton dominance (four replicates for each lake) were compared with single assessments based on corresponding quantitative biovolume data. Cellular biovolumes were computed from measurements of cell dimensions taken from 10–25 randomly selected cells of each taxon in each sample. Concurrence in ratings of the dominant taxa was excellent among limnologists in samples from lakes with blooms (100%) and only decreased slightly (94%) in samples from lakes with more diverse communities. Relative assessments of dominance agreed with quantitative assessments of biovolume in 86 percent of the 80 determinations. The high degree of agreement justified the application of the rapid semi-quantitative assessment to the measurement of relative phytoplankton dominance in all 579 samples. All analyses were conducted by the same investigator (R. Last) to minimize subjectivity.

Severity of phytoplankton blooms was classed as mild, moderate, moderately severe, or severe based on chlorophyll *a* concentrations above a threshold of 10 μg/L (Table 1). Breakpoints chosen to separate the four categories were determined from linear regressions representing the interrelationships among chlorophyll *a* concentrations, total phosphorus concentrations, and water clarity measurements as reported by Lillie and Mason (1983).

Limnological data collection procedures and laboratory methods are detailed in Lillie and Mason (1983). Chlorophyll data represent trichromatic chlorophyll *a* (UNESCO equation), uncorrected for pheophytin (0.45 um membrane filters, homogenized 90% acetone extract, modification of Strickland and Parsons 1968). Total phosphorus concentrations were measured using acid digestion-molybdate colorimetry (Eisenreich et al. 1975).

Data analysis was conducted using SAS (SAS Institute, Inc. 1988). Values reported represent means ± 1 standard error unless otherwise stated. In order to evaluate whether phytoplankton succession had a significant impact on our results (i.e., whether phytoplankton dominance within specific bloom categories was independent of sampling date), we compared dominance frequency plots of each phytoplankton group for lakes sampled before and after August 8th (331 and 248 lakes, respectively). Logistic regression was used to test for differences in the relationship of phytoplankton

Table 1. Classification of phytoplankton blooms based on chlorophyll *a* concentrations.

Bloom Class	*Chlorophyll* a (*μg/L*)
Non-bloom	< 10
Mild	10–15
Moderate	15–30
Moderately-severe	30–50
Severe	> 50

Table 2. Taxonomic summary of algae by order, family, and genera for 579 Wisconsin lakes.

Taxonomic Group	Orders	Families	Genera
Chlorophyceae	5	14	36
Bacillariophyceae	2	9	21
Cyanophyceae	3	4	17
Desmidiaceae	–	1	14
Chrysophyceae	4	6	12
Euglenophyceae	1	1	4
Dinophyceae	1	4	4
Xanthophyceae	2	2	2
Cryptophyceae	1	2	2
Totals	19	43	112

dominance to chlorophyll concentration between early and late sampling periods. Importance values (Appendix A) represent the average of assigned weights given to relative dominance ratings (i.e., 1–9).

Results

One hundred twelve phytoplankton genera, representing 43 families and 19 orders, were identified from the 579 lake samples (Table 2). A copy of the laboratory identification sheet containing a complete list of genera and species and their relative abundance for each lake in the data set is available from the authors (in microfiche) upon request. Green algae (Chlorophyceae, including family Desmidiaceae = desmids) and diatoms (Bacillariophyceae) were represented by the most genera. Only 17 blue-green (Cyanophyceae) algal genera were recorded. Taxa richness within individual lakes ranged from 2 to 24 genera. Most genera were uncommon: 16 genera were found in only one lake, and 60 genera occurred in less than 5% of the lakes (Appendix A). Only 20 genera occurred in more than 25% of the lakes. *Cryptomonas*, a cryptomonad (Cryptophyceae), was the most common alga, occurring in 80% of the lakes. *Anabaena*, a filamentous blue-green alga, was the second most common genus. Also found to be relatively common were two green alga genera, *Scenedesmus* and *Oocystis*, a chrysophyte, *Dinobryon*, another cryptomonad genus, *Chroomonas*, two dinoflagellate genera, *Ceratium* and *Peridinium*, a desmid genus, *Staurastrum*, and another colonial blue-green genus, *Coelosphaerium*. *Fragilaria* and *Melosira* were the most common diatom genera.

Collectively, blue-green algae were the most frequently dominant taxonomic group, with mixed assemblages, dinoflagellates, and diatoms next in order of rank (Table 3). The rank order based on the percentage of lakes in which each of the various taxonomic groups of algae were rated as at least important (includes important, co-dominant, and dominant) did not differ substantially from that of the dominant group. Seven of the 20

Table 3. Phytoplankton dominance by major taxa classification in all 579 Wisconsin lakes. Numbers represent percent of lakes in which each taxonomic group was dominant or at least important.

Taxonomic Group	*Dominant*	*at least Important**
Cyanophyceae	32	57
Mixed assemblages	24	—
Dinophyceae	18	43
Bacillariophyceae	11	40
Cryptophyceae	5	22
Chrysophyceae	5	20
Chlorophyceae	3	21
Desmidiaceae	3	11
Euglenophyceae	< 1	3

* includes lakes in which taxa were rated as important, co-dominant, and dominant.

Table 4. Twenty most commonly dominant and important genera in survey of 579 Wisconsin lakes.

Genus	*Dominant*			*at least Important**		
	(N)	*(% lakes)*	*(Rank)*	*(N)*	*(% lakes)*	*(Rank)*
Anabaena	108	19	1	230	40	1
Peridinium	69	12	2	131	23	2
Aphanizomenon	48	8	3	109	19	6[t]
Microcystis	36	6	4	110	19	5
Ceratium	33	6	5	115	20	4
Cryptomonas	28	5	6	120	21	3
Melosira	28	5	7	90	16	8
Coelosphaerium	24	4	8	109	19	6[t]
Dinobryon	17	3	9	79	14	9
Staurastrum	14	2	10	39	7	14
Glenodinium	13	2	11	43	7	13
Tabellaria	13	2	12	47	8	11
Oscillatoria	13	2	13	37	7	15
Fragilaria	12	2	14	76	13	10
Synura	12	2	15	29	5	18
Chroococcus	9	2	16	31	5	17
Cyclotella	8	1	17	34	6	16
Aphanocapsa	7	1	18	19	3	20
Synedra	3	< 1	19	44	8	12
Asterionella	3	< 1	20	28	5	19

* includes lakes in which genus was rated as important, co-dominant, and dominant.
t designates a tie.

most frequently dominant and important genera were blue-greens (Table 4). *Anabaena*, *Aphanizomenon*, and *Microcystis* were the most frequently dominant blue-greens; *Peridinium*, *Ceratium*, and *Glenodinium* were dominant dinoflagellates; and *Melosira*, *Tabellaria*, and *Fragilaria* were the most frequently dominant diatoms.

Composition of Blooms. Thirty-six percent of the lakes in the survey had some form of bloom present at the time of sample collection (Table 5), and only 11% of the lakes had severe or moderately severe blooms. Sampling date (early versus late summer) did not have a significant influence on phytoplankton dominace. Logistic regression indicated blue-green dominance increased ($p = 0.0001$) with chlorophyll concentration during both time periods. There was also an interaction ($p = 0.02$) between chlorophyll concentration and time period, because at low chlorophyll levels, blue-green dominance was less frequent during the early than the late sampling period, while at high chlorophyll levels blue-green dominance was similar in both sampling periods. Nevertheless, the overall trend for blue-green dominance to increase with chlorophyll concentration was present in both time periods. Therefore, although the frequency of occurrence of blooms was higher in lakes sampled during late summer, the dominance structure of blooms was not different from that found in lakes sampled earlier in the summer. Blue-greens were the most commonly dominant group within all bloom categories (Table 4), regardless of sampling date. The

Table 5. Phytoplankton dominance of major taxa relative to bloom condition (number of lakes in each class shown in parentheses). Data represent % of lakes within each bloom category in which taxa were dominant or co-dominant.

Taxa Group	*Bloom Condition*				
	Non-bloom (368)	*Mild (73)*	*Moderate (74)*	*Mod.-Sev. (34)*	*Severe (30)*
Cyanophyceae	23	37	45	68	70
Bacillariophyceae	12	8	7	18	20
Mixed assemblages	26	27	19	15	20
Cryptophyceae	5	3	7	0	13
Chlorophyceae	5	0	0	3	8
Dinophyceae	19	18	23	18	3
Chrysophyceae	5	10	7	3	0
Desmidiaceae	4	1	3	0	0
Euglenophyceae	< 1	1	0	0	0

frequency of blue-green dominance increased from 37% during mild blooms to 70% during severe blooms (Fig. 3b). Dinoflagellates were frequently dominant, and chrysophytes were occasionally dominant during mild and moderate blooms (Table 5), but both declined in importance during severe blooms (Fig. 3g and 3c). Cryptophytes tended to be more frequently dominant during severe blooms. Diatoms and greens tended to be important or dominant during moderately severe and severe blooms.

A core of 34 genera were commonly associated with blooms. (Commonness here is defined as those genera that were categorized as present in at least 25% of the lakes or as dominant in at least one lake experiencing a bloom; see Table 6). *Anabaena, Aphanizomenon, Aphanocapsa, Cryptomonas, Melosira, Oscillatoria,* and *Microcystis* were common dominants of severe and moderately severe blooms. *Aphanizomenon, Anabaena,* and *Peridinium* were common dominants of mild and moderate blooms. While the frequency of occurrence or dominance of most bloom genera did not appear to be directly related to degree of bloom severity, some genera, such as *Anabaena, Aphanizomenon, Aphanocapsa, Aphanotheca, Melosira, Oscillatoria, Pediastrum,* and *Scenedesmus* were most often dominant during severe or moderately severe blooms. A few genera, including *Peridinium, Synura, Tabellaria,* and *Dinobryon,* were more commonly dominant during milder blooms.

Characteristics of lakes experiencing blooms. Lakes experiencing phytoplankton blooms tended to be larger and shallower than lakes without blooms (Table 7). Lakes with blooms also had shorter residence times and had substantially higher nutrient concentrations and turbidities than lakes without blooms. Of 71 lakes with total phosphorus concentrations above 50 µg/L, 85% had some form of bloom at the time of sampling (54% severe or moderately severe). Only 9% of the lakes with total phosphorus concentrations less than 10 µg/L had a bloom (none were severe or moderately severe). Lakes with severe blooms had lower total nitrogen/total phosphorus ratios (TN:TP) (low TN:TP is an indication of possible nitrogen limitation) than lakes without blooms.

Table 6. Frequency of occurrence of genera listed as dominant during blooms or occurring in greater than 25% of lakes within a bloom class. Data represent percentages of lakes within each bloom class in which genus was dominant (% frequency of occurrence based on presence/absence shown in parentheses).

Genus	*Bloom Condition*				
	Non-bloom	*Mild*	*Moderate*	*Moder.-Severe*	*Severe Bloom*
Anabaena	14 (58)	32 (67)	28 (72)	50 (85)	55 (83)
Aphanizomenon	5 (14)	12 (36)	18 (41)	22 (59)	24 (47)
Aphanocapsa	< 1 (6)	0 (3)	2 (15)	3 (18)	14 (23)
Aphanotheca	0 (2)	0 (3)	0 (8)	0 (18)	3 (17)
Ceratium	8 (45)	7 (52)	1 (41)	12 (50)	3 (53)
Chroococcus	2 (37)	0 (22)	0 (24)	3 (29)	3 (30)
Chroomonas	< 1 (49)	0 (41)	1 (38)	0 (62)	0 (33)
Coelosphaerium	5 (33)	5 (47)	5 (43)	3 (35)	7 (57)
Coelastrum	0 (11)	0 (27)	0 (28)	0 (21)	0 (30)
Crucigenia	0 (30)	0 (27)	0 (22)	0 (9)	0 (20)
Cryptomonas	6 (80)	3 (84)	8 (77)	0 (76)	14 (80)
Cyclotella	2 (39)	0 (14)	0 (19)	3 (18)	3 (10)
Cosmarium	< 1 (28)	0 (20)	0 (20)	0 (23)	0 (33)
Dictyosphaerium	0 (9)	0 (12)	0 (31)	0 (15)	0 (17)
Dinobryon	3 (57)	5 (56)	5 (38)	3 (12)	0 (3)
Euglena	0 (8)	2 (19)	0 (16)	0 (21)	0 (27)
Fragilaria	3 (38)	2 (44)	1 (39)	3 (35)	0 (13)
Glenodinium	4 (30)	0 (19)	1 (24)	3 (26)	0 (33)
Gloeotrichia	< 1 (2)	2 (6)	0 (0)	0 (0)	0 (0)
Mallomonas	0 (25)	0 (37)	2 (31)	0 (26)	0 (13)
Microcystis	8 (32)	2 (33)	9 (41)	9 (59)	14 (43)
Melosira	4 (28)	5 (41)	6 (46)	12 (53)	17 (73)
Oocystis	1 (62)	0 (49)	0 (38)	0 (29)	0 (50)
Oscillatoria	3 (14)	2 (19)	0 (16)	0 (21)	14 (53)
Pediastrum	< 1 (17)	0 (20)	0 (35)	0 (29)	0 (57)
Peridinium	15 (46)	16 (44)	23 (42)	3 (9)	0 (0)
Scenedesmus	0 (56)	0 (53)	0 (70)	3 (56)	7 (77)
Staurastrum	4 (37)	0 (40)	3 (58)	0 (38)	0 (50)
Stephanodiscus	1 (11)	0 (8)	0 (16)	0 (26)	0 (43)
Synedra	< 1 (30)	2 (27)	3 (24)	0 (24)	3 (13)
Synura	2 (12)	7 (18)	3 (10)	0 (3)	0 (3)
Tabellaria	4 (25)	3 (30)	0 (19)	0 (6)	0 (0)
Tetraedron	0 (22)	0 (30)	0 (26)	0 (15)	0 (27)
Trachelomonas	0 (12)	0 (19)	0 (23)	0 (24)	0 (27)

Perceived water color was dramatically impacted by blooms (Table 8). None of the 64 lakes with severe or moderately severe blooms appeared blue or clear. Among lakes with mild or moderate blooms, 30% appeared green, 48% appeared brown, 7% appeared as a mixture of colors, 7% were turbid, and only 8% were clear or blue in appearance. While lakes without blooms also were frequently classed as colored (13% green, 35% brown, 3% mixed, and 2% turbid), 93% of the 176 lakes identified as blue or clear did not have blooms.

Discussion

Blue-green algae were dominant or co-dominant in one-third to two-thirds of all lakes

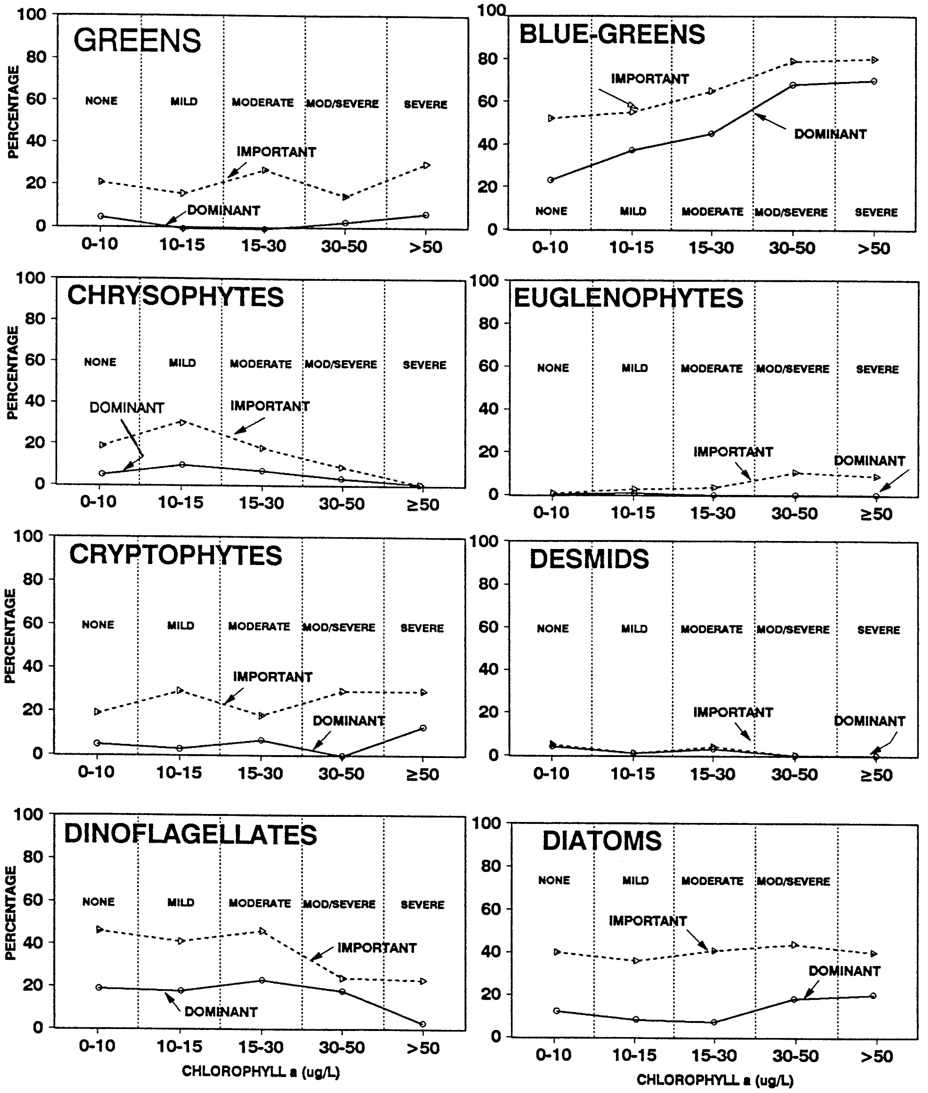

Figure 3. Relative dominance and importance of major taxa expressed as percentages of lakes within each bloom category that taxa were dominant (o) or important (^). Percent important also includes lakes in which taxa were dominant or co–dominant.

Table 7. Limnological conditions associated with phytoplankton blooms in Wisconsin lakes. Data represent means ± 1 SE.

		Bloom Condition					
Parameter	*Non-bloom*	*Mild*	*Moderate*	*Mod.-severe*	*Severe*	*All 579*	*661 Random***
(Chlorophyll *a* concentrations in µg/L)	5.6 ± 0.1	12.2 ± 0.2	20.6 ± 0.5	36.4 ± 0.8	82.3* ± 6.3	15.0 ± 1.3	14.3 ± 1.1
Physical:							
Size (ha)	116 ± 15	178 ± 78	943 ± 752	408 ± 175	338 ± 144	258 ± 98	242 ± 86
Mn Depth^p (m)	4.2 ± 0.2	3.8 ± 0.3	2.7 ± 0.2	3.2 ± 0.6	2.3 ± 0.3	3.8 ± 0.2	3.8 ± 0.2
Mx Depth (m)	8.9 ± 0.4	6.6 ± 0.5	5.4 ± 0.4	5.8 ± 0.7	4.3 ± 0.4	7.7 ± 0.2	7.7 ± 0.2
Residence^p (yr)	1.8 ± 0.2	1.0 ± 0.2	0.6 ± 0.1	0.6 ± 0.3	0.3 ± 0.1	1.4 ± 0.1	1.4 ± 0.1
Clarity (m)	2.7 ± 0.1	1.8 ± 0.1	1.3 ± 0.1	1.0 ± 0.1	0.6 ± 0.1	2.2 ± 0.1	2.2 ± 0.1
Chemical:							
Alkalinity (mg/L)	50.9 ± 2.8	54.5 ± 8.0	44.7 ± 6.3	71.8 ± 10.6	80.1 ± 13.2	53.2 ± 2.4	49.8 ± 2.2
Calcium (mg/L)	11.0 ± 0.6	12.7 ± 1.7	10.9 ± 1.4	16.7 ± 2.3	19.3 ± 2.8	12.0 ± 0.5	11.8 ± 0.5
Magnesium (mg/L)	7.1 ± 0.5	7.3 ± 1.3	6.1 ± 1.0	9.6 ± 1.8	10.9 ± 2.2	7.3 ± 0.4	7.2 ± 0.4
Chloride (mg/L)	3.2 ± 0.3	3.8 ± 0.7	4.3 ± 0.8	5.6 ± 1.0	8.0 ± 1.9	3.8 ± 0.2	3.8 ± 0.2
pH (units)	7.2 ± 0.1	7.2 ± 0.1	7.2 ± 0.1	7.5 ± 0.1	7.7 ± 0.2	7.2 ± 0.1	7.2 ± 0.1
Turbidity (JTUs)	2.4 ± 0.1	3.3 ± 0.3	4.2 ± 0.4	8.8 ± 2.4	10.8 ± 1.6	3.5 ± 0.2	3.4 ± 0.2
Color (units)	31.3 ± 1.7	40.9 ± 4.7	46.1 ± 4.5	52.2 ± 8.0	38.2 ± 3.9	35.9 ± 1.5	36.9 ± 1.5
Organic-N (mg/L)	0.49 ± 0.01	0.58 ± 0.04	0.72 ± 0.05	0.86 ± 0.08	1.21 ± 0.10	0.59 ± 0.02	0.59 ± 0.01
Total-N (mg/L)	0.69 ± 0.02	0.82 ± 0.04	1.06 ± 0.05	1.26 ± 0.07	2.09 ± 0.19	0.87 ± 0.02	0.85 ± 0.02
PO$_4$-P (µg/L)	7 ± 1	8 ± 1	20 ± 4	21 ± 4	82 ± 20	14 ± 1	13 ± 1
Total-P (µg/L)	19 ± 1	24 ± 2	38 ± 5	50 ± 7	149 ± 31	31 ± 2	30 ± 2

* excludes 1 lake with very high chlorophyll concentration.

** from Lillie and Mason 1983.

p = partial data, information not available for all lakes.

with blooms and in almost one-quarter of lakes without blooms. Collectively, blue-green genera were dominant among all categories of surface blooms. Blue-green dominance increased with the degree of bloom severity as measured by chlorophyll *a* concentration.

Although the frequency of blooms was higher in late summer, the dominance structure of phytoplankton communities did not differ substantially within bloom categories from early to late summer. Therefore, interpretation of relative phytoplankton dominance within specific bloom categories was not biased by the 63-day time period during which all 579 lakes were sampled. While the severity of blooms in many of the lakes sampled during the first half of the summer may have been higher had they been sampled during the later half of the summer sampling period, the composition of the blooms probably did not change significantly (at the group level). Such a conclusion is not altogether unexpected, as Bartell et al. (1978) reported relative constancy in species assemblages during the summer in extensive studies in Lake Wingra (Dane Co.). The frequency of occurrence of blooms and severity of blooms shown in Table 5 undoubtedly would have been higher if all lakes had been sampled during the later half of the sampling pe-

Table 8. Association between perceived color (visual appearance) and algal blooms in 579 Wisconsin lakes. Data represent numbers of lakes in each category.

		Bloom Severity				
*Perceived Color**	*Non-bloom*	*Mild*	*Moderate*	*Mod.-Sev.*	*Severe*	*Total*
Undescribed	9	1	0	0	1	11
Green	47	20	24	13	18	122
Brown	128	36	34	9	4	211
Turbid	9	4	6	3	0	22
Blue or Clear	164	11	1	0	0	176
Mixed	11	1	12	26	23	37
Subtotals	368	73	74	34	30	579

* some field observers did not differentiate between clear-green, green and turbid, or green and brown mixed.

riod. This, however, does not negate our conclusions regarding compositions of blooms.

These findings support conclusions regarding phytoplankton dominance derived from earlier cited studies of primarily eutrophic Wisconsin lakes. Blue-green algae are the single most important and dominant taxonomic group of algae in most Wisconsin lakes during summer months regardless of trophic state and, as such, should be targeted for management control.

The biomass of blue-greens in lakes has been shown to be directly correlated with TN:TP ratios under fixed light conditions (Smith 1986). No significant relationship was detected between TN:TP and the occurrence of blooms in our study; however, the ratio between mean TN and mean TP was lower in lakes with severe blooms than in lakes without blooms (Table 7). The progressive increase in frequency of occurrence of blue-green dominance with each level of bloom severity corresponds with the progressive decrease in TN:TP and agrees with Smith's (1983) findings. Furthermore, our data directly contradicts that of Canfield et al. (1989), who reported a decrease in frequency of blue-greens at TN:TP < 29. Light, temperature, inorganic nutrients, and zooplankton grazing can influence the relationship between blue-green dominance and TN:TP within individual lakes (McQueen and Lean 1987; Smith 1986; Spencer and King 1987).

Blooms were more common in large, shallow reservoirs or drainage lakes, in accordance with findings of other studies (Fee 1979). The greater internal recycling of nutrients, availability of sunlight, and thermal homogeneity of these systems provide a more optimum growth medium for blue-greens than that offered by deeper, thermally stratified lakes.

Limnological characteristics of the 579 lakes for which phytoplankton samples were available did not differ significantly from the characteristics of the entire 661 lakes in the random survey (Table 7). Therefore, findings regarding phytoplankton dominance reported in this survey and recommendations based on these data should be applicable to all Wisconsin lakes of similar size and depth. Based on the relationships between bloom severity and nutrient concentrations, as shown in Table 7, we propose the following in-lake phosphorus concentrations be established as thresholds for controlling blooms in Wisconsin lakes. An in-lake summer phosphorus concentration of

20 µg/L is an appropriate level to assure non-bloom conditions, while 30 µg/L TP is a more appropriate value to define the threshold between mild and moderate blooms. The former value corresponds with established spring phosphorus standards for southeastern Wisconsin lakes (SWRPC 1979) and with the results of the National Eutrophication Survey, which indicated that blooms did not occur in eastern United States lakes with less than 19 µg/L mean total phosphorus (Williams et al. 1977). Reduction of in-lake phosphorus concentrations below a given threshold value does not guarantee that a bloom will not occur (Welch 1989), as some lakes with phosphorus concentrations below the threshold will have blooms and some lakes with phosphorus concentrations above the threshold will not have blooms. Other factors, including differences in zooplankton grazing pressures, temperature, toxins, and other growth-limiting elements may interfere with the relationship. Threshold values may need to be adjusted according to a lake's geographic location to account for differences in phytoplankton dominance and response to nutrients that may occur among ecoregions (see Heiskary et al. 1987). Irrespective of the circumstances, reducing in-lake phosphorus concentrations will certainly decrease the likelihood that a bloom will occur or will reduce its intensity and duration.

Welch (1989) proposed that the fraction of total algae comprised of blue-greens is a sensitive indicator of nutrient concentrations and, thus, would make a good alternative eutrophication index were it not for the lack of agreed-upon trophic state threshold values. Based on the data collected in this study, a value of 25% blue-greens (by biovolume) may be an appropriate threshold criterion. Blue-greens were dominant (represented more than 25% of the total biovolume) in more than 50% of the lakes where chlorophyll *a* concentrations exceeded 30 µg/L. The 30 µg/L chlorophyll *a* concentration corresponds with our bloom classes of moderately severe and severe and matches the criterion for blooms established by Walker (1985).

Perceived water color (or visual appearance) has particular significance to lake managers in indicating blooms. In most cases, lakes that appear blue or clear do not have a bloom. Conversely, a green appearance to a lake does not necessarily signify a bloom as some lakes have a natural clear-green appearance. Likewise, while a brown appearance often corresponds with a diatom bloom, many lakes have a brown or yellow-brown stained appearance due to high concentrations of organic acids. However, if a lake's appearance changes from blue/clear to green, brown, or turbid, there is a very good probability that a phytoplankton bloom is occurring and that chlorophyll *a* concentrations exceed 10 µg/L. These color observations may not apply to other regions, but similar relationships may be established through direct observations. As such, general observations of water color can have a very important role in monitoring the trophic condition of a lake. Historical observations of blue or clear water color may be safely regarded as being indicative of good water quality (chlorophyll less than10 µg/L).

Lastly, the results of this survey demonstrate the utility of rapid subjective analysis of summer phytoplankton community compositions (in conjunction with other water quality data) as an informative monitoring tool in assessing water quality. Therefore, monitoring phytoplankton community compositions may be useful in measuring the effectiveness of agency-mandated nutrient control programs and lake restoration efforts.

Appendix A. Frequency of occurrence (as %), number of occurrences by relative dominance classification, and relative importance values for all phytoplankton genera found in 579 Wisconsin lakes during the summer of 1979.

Genera	Class*	Freq. of Occur.	Rare (1)	Present (3)	Import- ant (5)	Co- dominant (7)	Dominant (9)	Importance Values	
								State- wide	Lakes where present
Actinastrum	CHLO	2.8	-	10	4	-	-	0.09	3.57
*Amphora**	BACI	0.9	1	2	2	-	-	0.03	3.40
Anabaena	CYAN	64.0	24	116	122	62	46	3.15	4.92
Aphanizomenon	CYAN	24.6	4	29	61	26	22	1.34	5.44
Ankistrodesmus	CHLO	4.0	2	18	1	-	-	0.11	2.90
Aphanocapsa	CYAN	8.5	-	28	12	4	3	0.34	4.21
Aphanotheca	CYAN	4.8	-	20	5	1	-	0.16	3.50
Arthrodesmus	DESM	16.3	-	74	15	2	1	0.55	3.49
Arthrospira	CYAN	0.2	-	1	-	-	-	0.01	3.00
Asterionella	BACI	14.0	6	47	25	1	2	0.51	3.67
*Bambusina**	DESM	0.3	-	-	1	-	1	0.02	7.00
Botryococcus	CHLO	0.3	-	2	-	-	-	0.01	3.00
*Caloneis**	BACI	0.2	-	1	-	-	-	0.01	3.00
Carteria	CHLO	0.2	-	-	1	-	-	0.01	5.00
Ceratium	DINO	45.8	13	137	82	20	13	1.88	4.11
Chlamydomonas	CHLO	9.1	20	28	7	1	1	0.27	2.72
Chlorogonium	CHLO	0.9	-	5	-	-	-	0.03	3.00
Chroococcus	CYAN	33.0	1	157	22	5	4	1.13	3.46
Chroomonas	CRYP	46.7	2	252	12	2	-	1.44	3.10
Chrysidiastrum	CHRY	0.2	-	1	-	-	-	0.01	3.00
Chrysococcus	CHRY	0.2	-	-	1	-	-	0.01	5.00
Chrysosphaerella	CHRY	1.7	-	5	4	-	1	0.08	4.40
Closteriopsis	CHLO	0.5	-	1	2	-	-	0.02	4.33
Closterium	DESM	6.1	-	29	4	-	-	0.19	3.24
Coelosphaerium	CYAN	37.5	-	106	85	17	7	1.60	4.29
Coelastrum	CHLO	17.3	1	92	5	-	-	0.52	3.07
*Cocconeis**	BACI	4.8	-	23	3	-	-	0.15	3.23
Cosmarium	DESM	26.1	44	99	7	-	1	0.67	2.55
Crucigenia	CHLO	27.2	-	144	11	-	-	0.84	3.14
Cryptomonas	CRYP	79.9	2	338	92	15	13	2.94	3.68
Cyclotella	BACI	30.4	14	128	26	2	6	1.03	3.39
Cymatopleura	BACI	0.2	-	1	-	-	-	0.01	3.00
*Cymbella**	BACI	4.3	-	20	5	-	-	0.15	3.40
Dactyloccopsis	CYAN	1.7	1	7	1	-	1	0.06	3.60
Desmidium	DESM	0.5	-	2	1	-	-	0.02	3.67
*Diatoma**	BACI	0.2	-	1	-	-	-	0.01	3.00
Dictyosphaerium	CHLO	12.8	-	61	13	-	-	0.43	3.35
Dimorphococcus	CHLO	0.5	-	2	1	-	-	0.02	3.67
Dinobryon	CHRY	49.0	19	185	62	5	12	1.78	3.63
Elakotothrix	CHLO	1.7	-	10	-	-	-	0.05	3.00
*Epithemia**	BACI	0.9	-	4	1	-	-	0.03	3.40
Erkenia	CHRY	3.5	2	18	-	-	-	0.10	2.80
Euastrum	DESM	3.8	2	19	1	-	-	0.11	2.90
Eudorina	CHLO	12.6	5	59	12	-	-	0.42	3.18
Euglena	EUGL	12.1	17	44	8	-	1	0.34	2.83
Fragilaria	BACI	37.2	15	125	64	8	4	1.39	3.71
Franceia	CHLO	0.2	-	1	-	-	-	0.01	3.00
Glenodinium	DINO	28.0	6	111	30	5	8	1.03	3.68
Gloeocystis	CHLO	1.0	-	4	1	-	1	0.04	4.33
Gloeothece	CYAN	0.5	-	2	1	-	-	0.02	3.67
Gloeotrichia	CYAN	2.1	-	6	4	1	1	0.09	4.50
Golenkinia	CHLO	0.7	-	4	-	-	-	0.02	3.00
*Gomphonema**	BACI	2.8	-	15	1	-	-	0.09	3.12
Gonatozygon	DESM	0.3	-	2	-	-	-	0.01	3.00
Gymnodium	DINO	5.2	-	26	4	-	-	0.17	3.27
*Gyrosigma**	BACI	0.2	1	-	-	-	-	0.01	1.00

Genera	Class	Freq. of Occur.	Rare (1)	Present (3)	Import-ant (5)	Co-dominant (7)	Dominant (9)	Importance Values State-wide	Importance Values Lakes where present
Hyalobryon	CHRY	0.2	-	1	-	-	-	0.01	3.00
Hyalotheca	DESM	0.2	-	-	1	-	-	0.01	5.00
Kirchneriella	CHLO	4.2	-	24	-	-	-	0.12	3.00
Lagerheimia	CHLO	2.2	-	13	-	-	-	0.07	3.00
Lepocinclis	EUGL	0.5	-	2	-	-	1	0.03	5.00
Lyngbya	CYAN	5.4	1	17	12	1	-	0.21	3.84
Mallomonas	CHRY	26.6	16	129	8	1	-	0.78	2.92
Merismopedia	CYAN	6.6	-	32	4	1	1	0.23	3.28
Micractinium	CHLO	0.9	-	5	-	-	-	0.03	3.00
Micrasterias	DESM	0.9	-	5	-	-	-	0.03	3.00
Microcystis	CYAN	35.3	8	86	74	20	16	1.59	4.50
Melosira	BACI	35.8	23	94	62	20	8	1.43	3.98
Monomastix	CHRY	8.8	-	47	4	-	-	0.28	3.16
*Navicula**	BACI	10.0	2	52	3	-	1	0.31	3.03
Nephrocytium	CHLO	1.9	-	11	-	-	-	0.06	3.00
Nodularia	CYAN	0.2	-	1	-	-	-	0.01	3.00
Ochromonas	CHRY	1.2	-	7	4	-	-	0.07	3.73
Onychonema	CHLO	0.7	-	3	1	-	-	0.02	3.50
Oocystis	CHLO	55.0	187	120	8	1	2	1.06	1.65
Ophiocytium	XANT	0.7	-	4	-	-	-	0.02	3.00
Oscillatoria	CYAN	17.6	19	46	24	7	6	0.66	3.72
Pandorina	CHLO	7.1	-	34	6	-	1	0.24	3.28
Pediastrum	CHLO	22.8	16	99	16	1	-	0.69	3.03
Peridinium	DINO	40.8	1	102	62	16	53	2.08	5.11
Phacus	EUGL	6.9	2	36	2	-	-	0.21	3.00
Phormidium	CYAN	0.7	-	3	1	-	-	0.02	3.50
*Pinnularia**	BACI	0.5	-	3	-	-	-	0.02	3.00
Pleodorina	CHLO	0.3	-	1	1	-	-	0.01	4.00
Pleurotanium	DESM	0.9	-	3	1	-	1	0.04	4.60
Psephonema	XANT	0.9	-	5	-	-	-	0.03	3.00
Quadrigula	CHLO	13.3	-	75	-	-	2	0.42	3.16
Rhabdoderma	CYAN	1.9	-	10	-	-	1	0.07	3.55
Rhoicospheria	BACI	0.3	-	2	-	-	-	0.01	3.00
*Rhopalodia**	BACI	1.0	-	6	-	-	-	0.03	3.00
Scenedesmus	CHLO	58.8	110	211	16	2	1	1.46	2.49
Selenastrum	CHLO	3.6	-	20	1	-	-	0.11	3.10
Schroderia	CHLO	7.3	-	42	-	-	-	0.22	3.00
Sorastrum	CHLO	0.5	-	3	-	-	-	0.02	3.00
Sphaerocystis	CHLO	16.6	11	70	12	2	1	0.53	3.17
Spirogyra	CHLO	13.8	1	1	3	2	1	0.07	5.25
Spirotaenia	DESM	0.2	-	1	-	-	-	0.01	3.00
Spondylosium	DESM	7.8	9	26	9	-	1	0.24	3.13
Staurastrum	DESM	40.5	60	135	25	6	8	1.21	3.00
*Stauroneis**	BACI	0.2	-	1	-	-	-	0.01	3.00
Stephanodiscus	BACI	13.8	13	53	11	-	3	0.44	3.18
Synedra	BACI	28.2	2	115	41	2	1	0.99	3.53
Synura	CHRY	11.8	-	39	17	6	6	0.52	4.26
Tabellaria	BACI	22.7	7	77	34	3	10	0.90	3.96
Tetraedron	CHLO	23.2	26	104	4	-	-	0.62	2.67
Trachelomonas	EUGL	15.6	14	70	6	-	-	0.44	2.82
Treubaria	CHLO	0.2	-	1	-	-	-	0.01	3.00
Ulothrix	CHLO	7.4	7	24	17	1	-	0.30	3.49
Uroglena	CHRY	0.9	-	-	3	-	2	0.06	6.60
Uroglenopsis	CHRY	0.2	-	1	-	-	-	0.01	3.00
Volvox	CHLO	1.4	-	3	4	1	-	0.06	4.50
Xanthidium	DESM	2.8	-	13	1	1	1	0.10	3.75

**taxa believed to be primarily epiphytic and only incidently found in the plankton (i.e. tychoplankton).
Taxon codes: BACI=Bacillariophyceae, CHLO=Chlorophyceae, CHRY=Chrysophyceae, CRYP=Cryptophyceae, CYAN=Cyanophyceae, DESM=Desmidiaceae, DINO=Dinophyceae, EUGL=Euglenophyceae, XANT=Xanthophyceae.

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This study was conducted by staff of the Bureau of Research, Water Resources Research Section, with the assistance of numerous individuals who were acknowledged in Lillie and Mason 1983. We wish again to express our thanks to those individuals who conducted the field collections and completed the laboratory analyses. Co-author Robert Last diligently performed taxa identifications and determined relative dominance on all 579 samples over a period of several years and deserves most of the credit for seeing this project through to the end. We also thank I. Marx-Olson for assistance in computer data entry and D. Knauer for critical review of the manuscript. Thanks are also extended to W. Sloey, an anonymous reviewer, and the Editor for their many useful suggestions.

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Richard Lillie, Paul Garrison, John Mason *(retired) are Research Scientists with the Wisconsin Department of Natural Resources, Bureau of Research, Water Resources Research Section, Monona, Wisconsin.*

Paul Rasmussen *is a Biometrician with WDNR Bureau of Research, Monona, Wisconsin.*

Robert Last *was a Natural Resources Specialist with the Water Resources Research Section.*

Charles A. Long and John E. Long

Discriminant analysis of geographic variation in long-tailed deer mice from northern Wisconsin and Upper Michigan

Abstract *Identification of morphologically similar long-tailed mice* (Peromyscus spp.) *from the forests of northern Wisconsin and Upper Michigan was clarified by application of statistical analysis. Use of student t-tests, bivariate plots, Dice squares, analysis of variance, and a stepwise discriminant analysis revealed three distinctive populations. Previously, mice from this region were identified as* P. leucopus *or* P. maniculatus gracilis, *and neither was very clearly distinctive from the other. The best characters used to identify these mice were ear length, length of rostrum, and length of tail. Other characters varied significantly from group to group, but incisive foramina length, cranial depth and cranial breadth (previously given heavy weight by taxonomists) were the least reliable. Discriminant coefficients were developed that may be used in future studies classifying approximately 2,000 unidentified museum specimens, based upon the canonical functions that segregate the three groups best. Predictability based on probability of best fit, and next best fit, ranged from 82 to 90 percent. The deer mice from three isles in Lake Michigan closely resembled typical* P. maniculatus maniculatus *from Labrador even more than they resembled the northern Lake Superior mice formerly assigned to* P. m. gracilis. *Northern specimens approach* maniculatus *but the southernmost long-tailed deer mice are smaller. Six recently collected specimens from Washington Island, in Lake Michigan, resemble* P. leucopus *from central Wisconsin and are the first record of* P. leucopus *on any island in Lake Michigan.*

Aside from the confusing and well-known resemblance of the forest deer mouse (*Peromyscus maniculatus gracilis*) to the common white-footed mouse (*Peromyscus leucopus*), Long (1978) noted slight clinal variation in *P. m. gracilis* from north to south and documented differences (particularly in longer rostrum) in *P. m. gracilis* on St. Martin Island, Michigan. Cursory examination of *P. m. gracilis* specimens from the Apostle Islands revealed cranial differences from many Wisconsin *gracilis*, especially the narrower and shorter rostrum of the Apostle Islands *gracilis*. This form resembled *Peromyscus maniculatus maniculatus* from Ontario, as figured by Osgood (1909) in his classic taxonomic revision of *Peromyscus*. The difficulty in segregating two or perhaps three similar deer mice has hindered a proper classification (at the University of Wisconsin-Stevens Point [UWSP] Museum of Natural History) of nearly 2,000 specimens from Wisconsin and some from the Upper Peninsula of Michigan. Over the last decade, students who have regularly collected *gracilis* on Washington Island began to catch some specimens that appeared to be *P. leucopus*, hitherto unknown on any island in Lake Michigan.

In southern Wisconsin, Stromberg (1979) used discriminant analysis to distinguish *P. leucopus* from *P. m. bairdii*, a small, short-tailed prairie form inhabiting sandy soils of southern and western Wisconsin. However, these two species are easily identified even as young animals (Long 1968). Greater difficulty is encountered in separating *P. m. gracilis* from the Canadian race *P. m. maniculatus*, and both of them from *P. leucopus*.

Why is it that in the past two subspecies of long-tailed deer mice (*P. maniculatus*) have been recognized in Michigan but only one has been noted in Wisconsin? Baker (1983) followed Burt's (1948) earlier classification of Michigan mammals, and Burt, without comment, had followed Osgood's (1909) monographic revision of *Peromyscus*. Osgood reported *P. m. maniculatus* from Isle Royale and *P. m. gracilis* from both Upper and Lower Michigan. However, for nearby Wisconsin mice, Osgood (1909) and Jackson (1961) used only *gracilis*, and Minnesota workers, without comment, used *gracilis* there (Gunderson and Beer 1953; Hazard 1982). We, on the other hand, expected that *P. m. maniculatus* ranged southward into Wisconsin.

The only samples available to Osgood from northern Michigan and Wisconsin were a large series (N=55) from Isle Royale (this island lies very near the Ontario shore of southern Canada, and these mice seem referable to Canadian *maniculatus*) and a few specimens from all of Michigan (13) and Wisconsin (7). As classic and extensive as Osgood's (1909) revision was, his samples were inadequate to classify and map the detailed geographic distributions of these closely similar mice in this region. In our study we analyzed variation by rigorous statistical tests of the long-tailed kinds present in northern Wisconsin, the Upper Peninsula of Michigan, and islands in Lake Superior and Lake Michigan.

Taxonomic Characters

Typical *P. leucopus* may be distinguished from *P. m. gracilis* by several visible characters if one compares a series of specimens of one mouse or the other, or if any given individual possesses several trenchant characters. But if the collection is mixed—or if a specimen is unusual or, as is more often the case, subadult—then correct identification may be impossible. Mismeasured specimens, skins lacking skulls, or skulls lacking skins complicate taxonomic identification.

The white-footed mouse (*P. leucopus*) is most recognizable by a short tail (both actual and relative to body length) that is sparsely haired. Vestigia of ancient reptilian scales are commonly visible on it, and the sparse hairs seem dingy. In those specimens having such tails, the tail is not sharply bicolor nor does the tip ever bear a pencillate tuft. In those *P. leucopus* having bright-colored and well-haired tails, the short length helps in identification.

Peromyscus maniculatus gracilis, originally described by its elongate tail and only tentatively ascribed to "Michigan," has enormous ears, prominent and elongated whiskers (vibrissae), and a long snout. *P. m. maniculatus*, the nominate race of deer mouse ranging across much of eastern Canada, and reported by Osgood from Isle Royale in Lake Superior, resembles *gracilis* in long, pencillate tail and long ears. Reportedly it is darker in color. Owing to hybridization in southern Ontario, any distinctive features there in *P. m. maniculatus* reportedly are merged somewhat with *P. m. gracilis* (Osgood 1909).

Peromyscus maniculatus maniculatus has never been documented in Wisconsin, nor has anyone since Osgood bothered to investigate that possibility. However, skulls from the Apostle Islands and from nearby Drummond, Wisconsin, appreciably differ from those of *P. m. gracilis* from the Lake Michigan Isles (Washington Island, St. Martin Island, and Rock Island, Long 1978). We considered that the former sample might be referable instead to nearby Canadian *P. m. maniculatus*. The shape of their rostra, indeed, resembles the figured rostrum chosen for nominate *P. m. maniculatus* by Osgood (1909).

Osgood (1909) selected representative skulls to illustrate qualitative characters of form. In *P. leucopus* the rostrum is short and rather pinched anteriorly, and as a consequence the incisive foramina (Fig. 1) on the hard palate are likewise constricted anteriorly. In either *P. m. maniculatus* or *P. m. gracilis*, or in their intergrades, the rostrum is longer and the incisive foramina more nearly parallel, i.e., straight sided. In *P. m. gracilis*, the rostrum is supposed to be quite elongate and not so narrow as in *P. leucopus* or *P. m. maniculatus*.

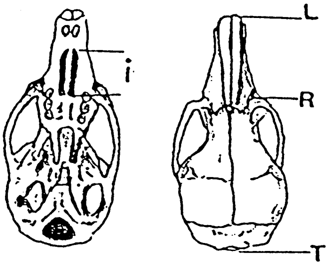

Fig. 1. Cranial measurements of *Peromyscus*. RL, length of rostrum; TL, total length or greatest length of skull; i, length of incisive foramina. The cranial width is measured across and including the convex bulges of the cranium immediately posterior to the zygomatic arches. The cranial depth is measured from the top of the braincase to its base, between (not including) the auditory bullae.

Rostral shape and incisive foramen length have been used by Hazard (1982) to distinguish *P. m. gracilis* from *P. leucopus*. Overlap of these characters between samples was considerable in Wisconsin. Burt (1948) reported the infraorbital canal as distinctive in form in Michigan *P. m. gracilis*, but in Wisconsin no difference in this character is apparent in *gracilis* and *leucopus* (Jackson 1961; Long 1974). Choate (1973) found rostral breadth useful in distinguishing these species, but in our series there was no significant difference in rostral breadth between *gracilis* and Portage County specimens of *leucopus*.

Methods

In this article, the following terms refer to the geographical areas where the large samples of specimens were taken:

Lake Michigan Isles—Washington Island, Rock Island, and St. Martin Island, all found in Lake Michigan near the northeastern Wisconsin shore.

Central Wisconsin—Portage County

Lake Superior—Outer Island and Stockton Island (both members of the Apostle Islands in Lake Superior near the northern Wisconsin shore); and Drummond on the mainland in northern Wisconsin.

Measurements used in this study included the standard measurements of skin labels, of which only the length of ear and tail proved useful. Cranial measurements (Fig. 1) included total length of skull; length of rostrum measured from the tips of the nasals to the slight constriction anterior to the zygoma; length of the incisive foramina; and in some samples cranial width, measured immediately posterior to the zygomata, and cranial depth (not including the auditory bullae). C. A. Long made all the cranial measurements. No size differences were noted between males and females. Young animals were excluded. These were recognized by juvenal pelage, small weak skulls, unworn upper molars, and an open basioccipital-basisphenoid suture.

Most of the specimens were from Wisconsin and Upper Michigan and are preserved in the UWSP Museum of Natural History. Eight specimens of typical *P. m. maniculatus* from Labrador were borrowed from the United States National Museum of Natural History (USNM). Also borrowed were Jackson's (1961) two specimens of *P. m. gracilis* caught in the Sheboygan Marsh in southern Wisconsin, a population disjunct from the geographic range of northern *gracilis.*

Skulls appreciably larger from the Lake Michigan Isles were compared (student t-tests of cranial width) with skulls of specimens from Outer Island, Lake Superior, and from Stockton Island in Lake Superior and nearby Drummond on mainland Wisconsin. Means of cranial width were calculated to compare the samples from Outer Island with those from Stockton-Drummond, as well as to compare Stockton mice with Drummond mice. These comparisons were made to consolidate the Lake Superior populations as a homogeneous group, even though the group includes insular and mainland populations. Means and standard deviations were calculated and compared from the Lake Superior population, the Michigan Isles population, numerous *P. leucopus* from Portage County in central Wisconsin, and other appropriate populations to study geographic variation along a generally northwest to southeast dimension or transect.

These three groups—the Lake Superior group, the Lake Michigan Isles group, and central Wisconsin *leucopus*—were analyzed by stepwise discriminant function analysis, using the aforementioned five linear variables (length of ear, tail, skull, rostrum, and incisive foramina) and ordering the characters by their apparent usefulness (F values) in identification. All specimens that did not fit well within their groups were flagged. Allocation to a group was determined by the probability of best fit, as well as by examining the specimens that showed the second highest probability for fit. Scatter plots were mapped using two discriminant functions to segregate the three groups. The data were evaluated to determine the percentage that fit in their appropriate groups, and discriminant coefficients were calculated for use in future testing. The three groups were used as standards against which some small samples were compared. One such sample reported herein was a collection of six mice that were tentatively identified in our study as *P. leucopus*, previously unknown in the fauna of Washington Island, or on any island in Lake Michigan or Lake Superior. The USNM series of typical *P. m. maniculatus* from Labrador was assigned to one of the three groups by use of the Fisher coefficients.

Results and Discussion

Measurements are given in Table 1 for the three large populations or groups analyzed (Lake Superior, Michigan Isles, and central Wisconsin). Although there is overlap in most of the measurements, *P. leucopus* can be identified usually by smaller dimensions, except for length of skull and rostral width. When length of the ear is plotted against length of tail (Fig. 2), there is clear separation of the Lake Michigan Isles mice from *P. leucopus.* Some collections of *Peromyscus* from Washington Island made in recent years scatter across the graph, and some specimens suspected to be *P. leucopus* indeed fit among the *leucopus* (central Wisconsin group).

The same results were found by plotting incisive foramina length against length of rostrum (Fig. 3). In this comparison numerous recently taken specimens fit among the *leucopus* specimens; none of them fit in the *gracilis* camp.

Transects of mice northwest to southeast (Figs. 4–7) reveal overlap of all characters chosen, except that the Lake Michigan Isles *gracilis* tended toward high values and differed most from *P. leucopus.* (Cranial width was not measured in *leucopus*, Fig. 7.)

In a t-test the mice from the Lake Michigan Isles were broader across the cranium than those in the Lake Superior group (12.32 ± .43 versus 11.95 ± .24, $p < 0.001$). Five specimens (of 22) in the Lake Michigan Isles group had open sutures (indicating subadult age), but their skulls were broader all the same. We expected the Lake Superior group to have the wider skulls. The two populations did not differ in total length of skull (26.5 versus 25.78 mm, $p < 0.001$) or tail length (83.1 versus 83.6, $p < 0.001$). Lake Michigan Isles mice also had wider skulls than those mice combined from Stockton Island and Drummond, but the latter two samples were significantly wider than the mice from nearby Outer Island. (The Stockton Island and Drummond mice did not differ significantly from one another.) Therefore, in cranial width the Lake Superior group was not strictly homogeneous.

Concerning cranial breadth or width, our study only proves that mice on Outer Island are narrow (though resembling our museum specimens from southern Ontario; see Fig. 7). Osgood's own figures and measurements do not confirm his claim that *P. m. maniculatus* has the wider skull, even though his representative specimens were collected in the eastern part of the range far from the zone of intergradation of that race with *P. m. gracilis.* The Labrador series we examined averaged 12.3 in the seven adults, which is but slightly wider than in Lake Superior group specimens (Table 1). We found no significant difference in tail length between the groups from Lake Superior and Lake Michigan (Table 1), or between Wisconsin deer mice and the Michigan *maniculatus* reported by Baker (1983).

In the analysis of variance, all five measured variables showed geographic variation, so that in the total analysis all three Wisconsin populations seemed distinct (Table 2).

Of the variables, ear length gave the highest F-value among the three groups (Table 2), but this field measurement is often slightly made in error. Hazard (1982) considered smaller ears as characteristic of *P. m. maniculatus.* However, the Labrador series of *maniculatus* averaged 19.7 mm. Short ear length statistically separates *P. leucopus* from the other two groups. Length of rostrum separates all three populations evenly. Small incisive foramina, short skull, and shorter tail separate *P. leucopus* out fairly well, except for the considerable overlap in all these variable traits (Table 1).

In the stepwise discriminant analysis, the variables were removed in the order listed in Table 2. Wilk's lambda varied from 0.54 to 0.31, all highly significant in length of ear and the other variables through incisive foramina.

The success in prediction of specimens for all the three groups (Fig. 8) exceeded 80 percent. Of 60 specimens from the Lake Michigan Isles, only 12 fit outside the group 1 sector, and eight fit better in the Lake Superior sector. Of 30 *leucopus* from central Wisconsin, 27 clumped together, and the remainder fit with the Lake Superior group. Of 20 specimens from the Lake Superior group, 15 clumped together. Three fit with the Lake Michigan specimens and two with central Wisconsin *leucopus.*

The Lake Michigan Isles mice had a predicted membership of 82 percent. *Peromyscus leucopus,* which is so difficult to identify by conventional characters, predicted very well with 90 percent strictly within its group. Most of the specimens that did not fit their appropriate group with highest priority did so as the *second* highest probability. Of the 12 in the Lake Michigan Isles group, six fit as a second probability. Of the three central Wisconsin mice, two fit as a second probability.

The six specimens tentatively identified in recent years as *P. leucopus* from Washington Island (hitherto unknown on any islands in Lake Michigan) identified closely with the central Wisconsin group (*P. leucopus*) (Fig. 9). A small group consisting of Washington Island mice not tentatively identified as *P. leucopus* but from the same recently obtained field collections (and including a few subadults) segregated poorly. The bivariate analysis (Figs. 2–3) also showed much overlap of characters in these recently collected specimens.

Fisher's Linear Discriminant Functions, useful as classification coefficients, are given in Table 3. The individual's measures are multiplied by the coefficients to weight them for taxonomic discrimination. Use of Fisher's coefficients surprisingly classified the two disjunct Sheboygan Marsh specimens with the Lake Superior deer mice, although the two skulls were so small and the ears so short they closely resemble *P. leucopus* (which now seems to be the only *Peromyscus* present in the Sheboygan Marsh). One of the two is not quite adult (USNM 227357). These two small skulls differ markedly from deer mice skulls of Lake Michigan Isles, geographically much nearer but isolated by water on islands of Lake Michigan. They are practically indistinguishable from a large sample recently examined from Lower Michigan (Long, unpublished).

The big surprise was the close resemblance of the Lake Michigan Isles group to the typical *P. m. maniculatus* from far away Labrador, rather than to mice nearer at Lake Superior. The resemblance was also close in color of the pelage. The Lake Superior group differed from the Labrador *P. m. maniculatus,* which was unexpected because mice from Ontario and nearby Isle Royale are referred to as *P. m. maniculatus.* All seven adults in the Labrador series fit with the Lake Michigan Isles group. They resembled *P. leucopus* least, which, of course, was to be expected.

Discriminant analysis weights the characters in the optimal way to allow the groups to segregate. Differences may or may not reflect speciation, and they must be perceived with caution. However, in Wisconsin, obvious but overlapping differences in the three groups justified the analysis. If the variation is spurious or drift-like, it is of interest all the same, because the resemblance to Labrador mice, which is very close, suggests that gracilis is a synonum of *P. m. maniculatus*. Such microgeographic variation may indeed be part of the problem (Ledehrle et al. 1985). On the other hand, the resemblance of Lake Michigan and Labrador mice may arise from effects of Pleistocene and early Holocene climate on the zoogeography of *Peromyscus maniculatus*.

The Canadian race *P. m. maniculatus* formerly may have been widespread, with some populations colonizing islands. Peripheral mainland populations may have evolved new characters, such as small size, leading perhaps to the geographic variation named *gracilis* by Osgood (1909) or described by us by using Osgood's name. Additional studies on electrophoretic variation in proteins, such as the work by Calhoun and Greenbaum (1991), may clarify the observed differentiation.

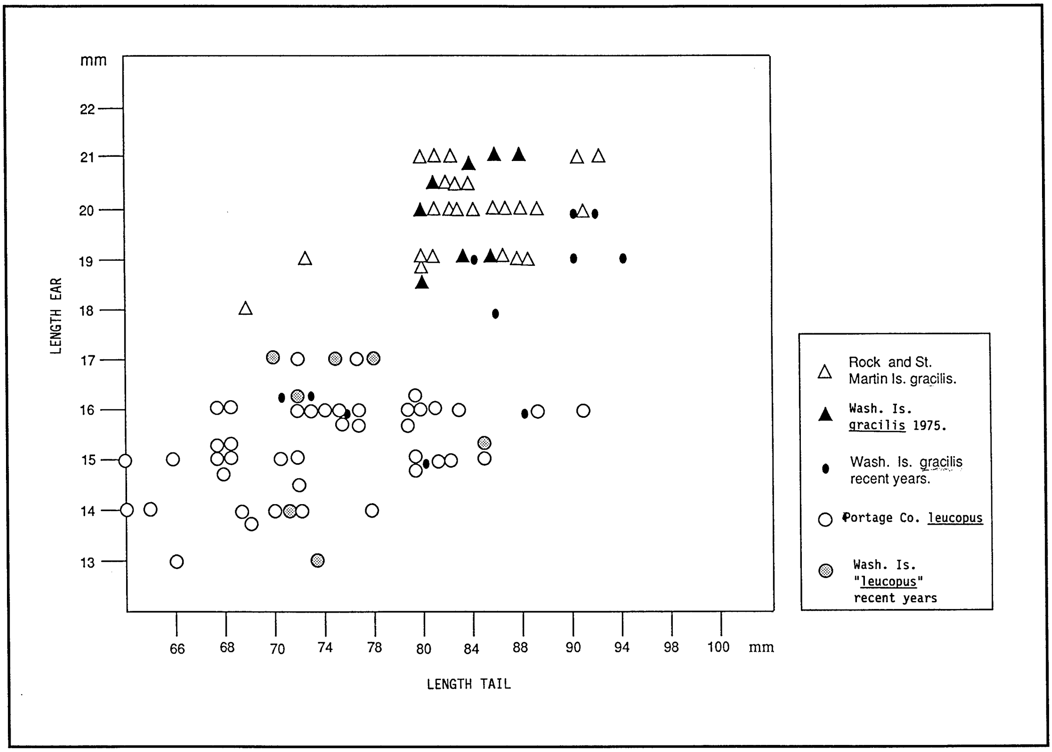

Fig. 2. Bivariate plot of length of ear and length of tail.

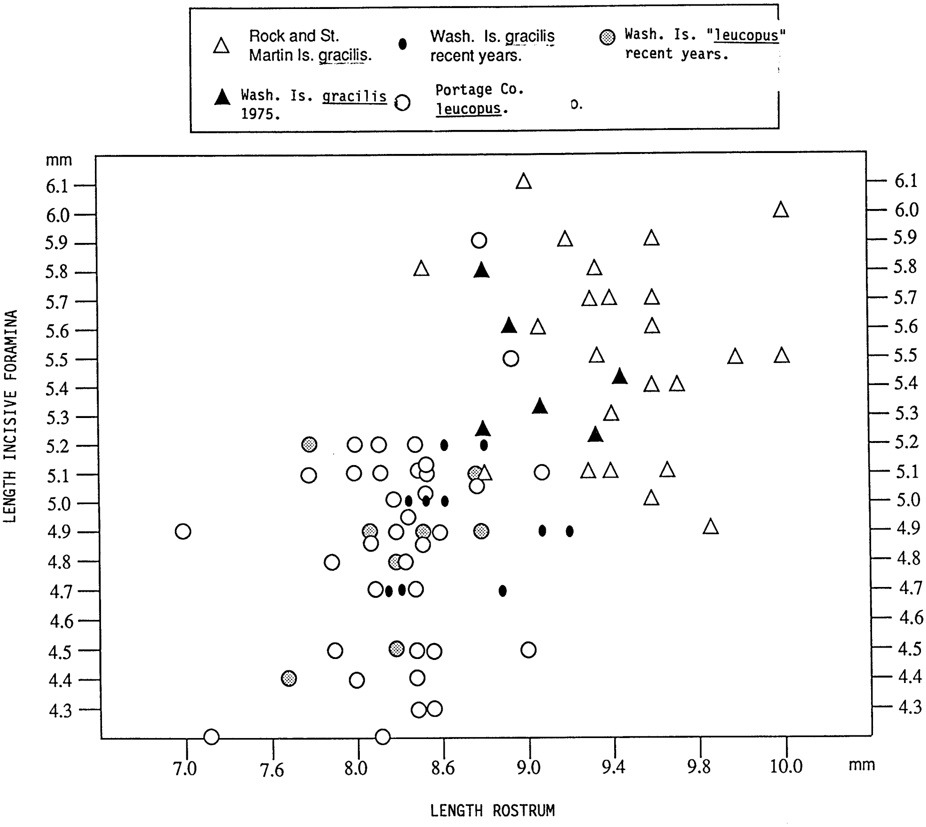

Fig. 3. Bivariate plot of incisive foramina length and length of rostrum.

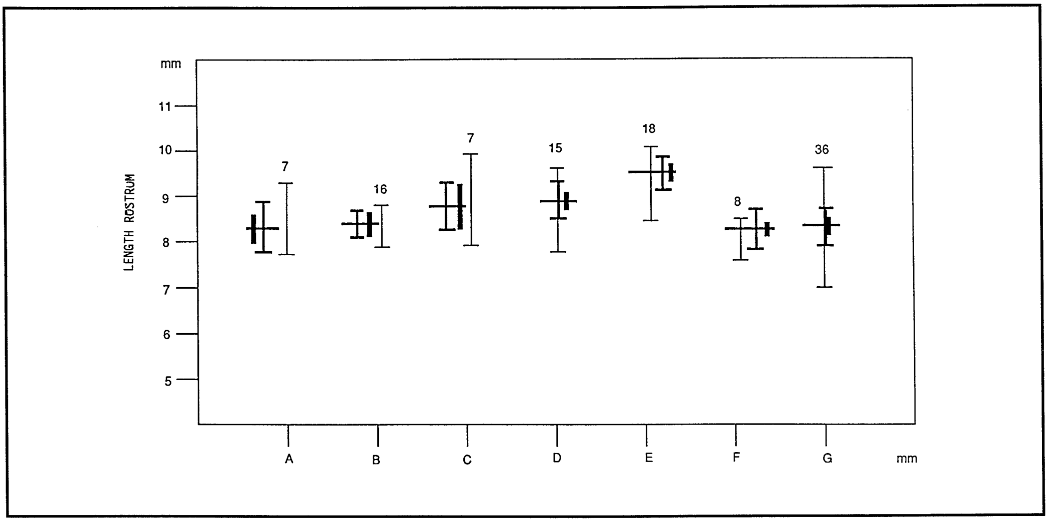

Fig. 4. Transect of deer mice localities based on rostral length, northwest to southeast. Modified Dice-squares (mean, the horizontal; N, sample size above the I-shaped vertical for observed range; standard deviation, the boldfaced I-shaped vertical; twice the standard error, the short thick, vertical. A, specimens from southwest Ontario; B, Outer Island, Apostle Islands, Wisconsin; C, Stockton Island, Apostle Islands; D, Drummond, Wisconsin; E, Lake Michigan: St. Martin Island, Rock Island, Washington Island (early years); F, Possible *P. leucopus* from Washington Island; G, *P. leucopus* from Portage County, Wisconsin.

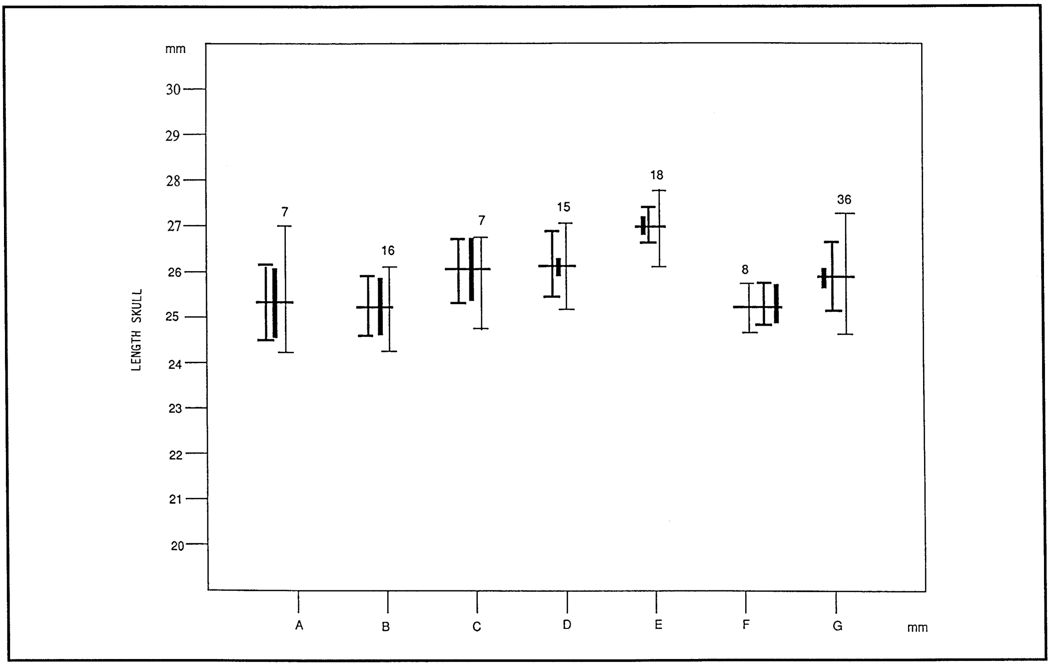

Fig. 5. Transect of deer mice localities based on total length of skull (see Fig. 4 for explanation).

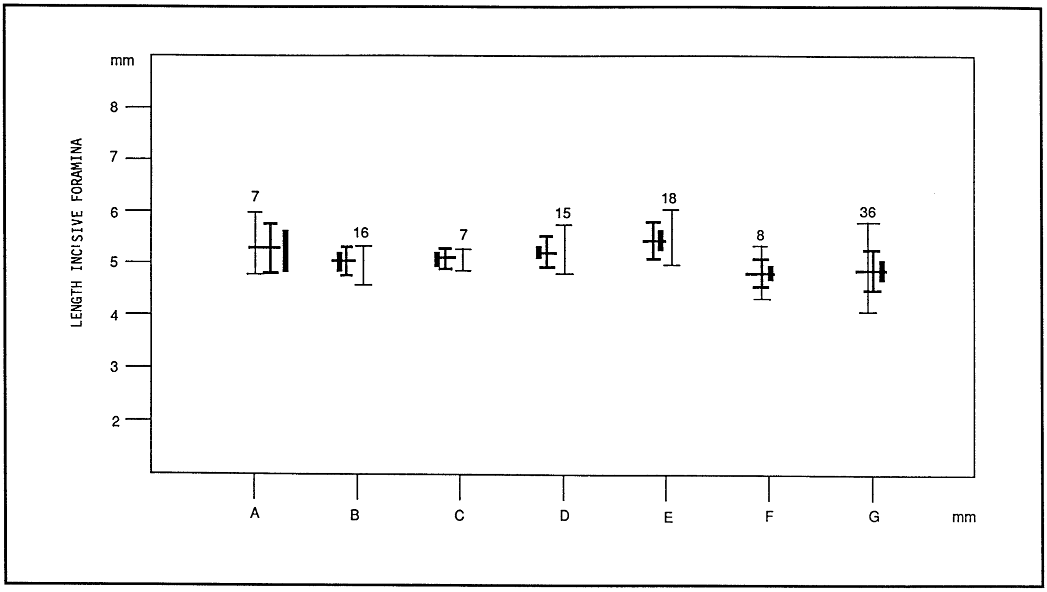

Fig. 6. Transect of deer mice localities based on length of incisive foramina (see Fig. 4 for explanation).

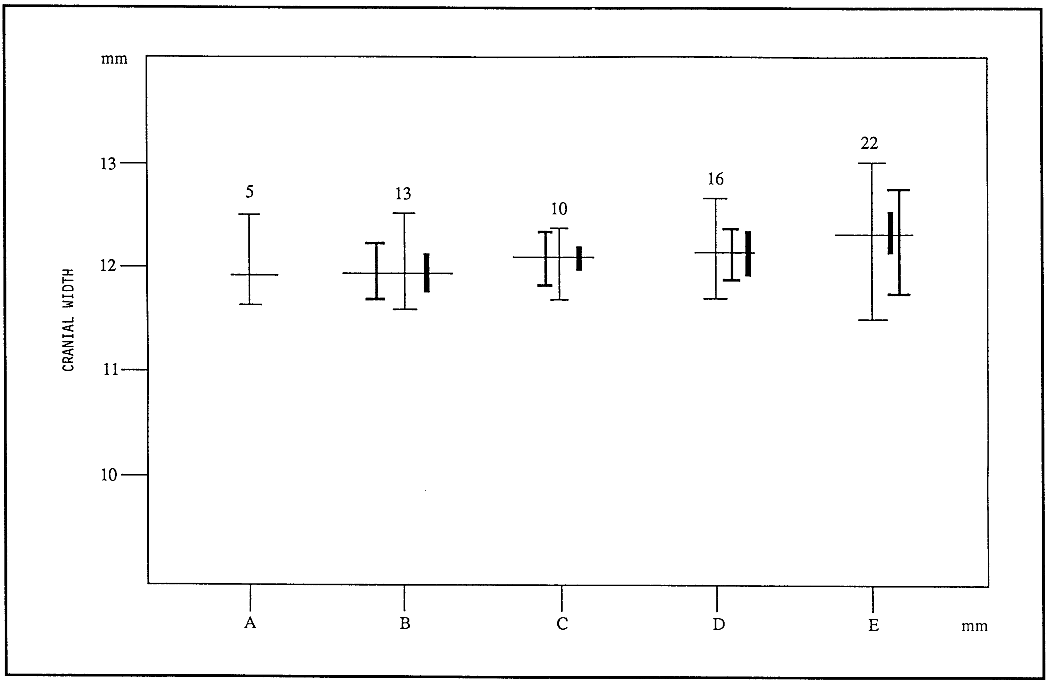

Fig. 7. Transect of deer mice localities based on cranial width (see Fig. 4 for explanation).

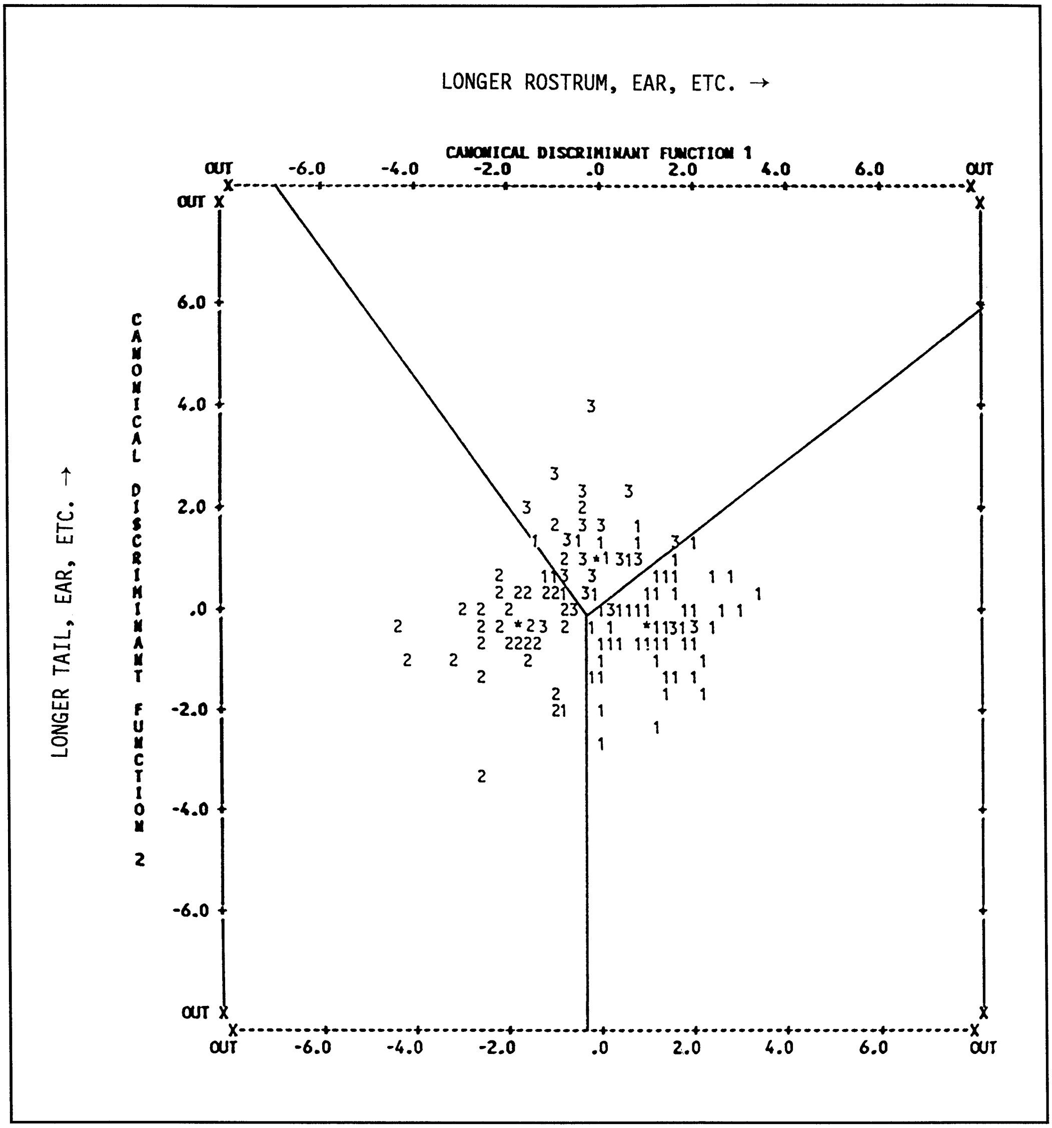

Fig. 8. Scatter plots of *Peromyscus* groups 1-3.
1 = Lake Michigan Isles
2 = Central Wisconsin (*leucopus*)
3 = Lake Superior
Values are canonical variates of discriminant functions. Asterisks are centroids.

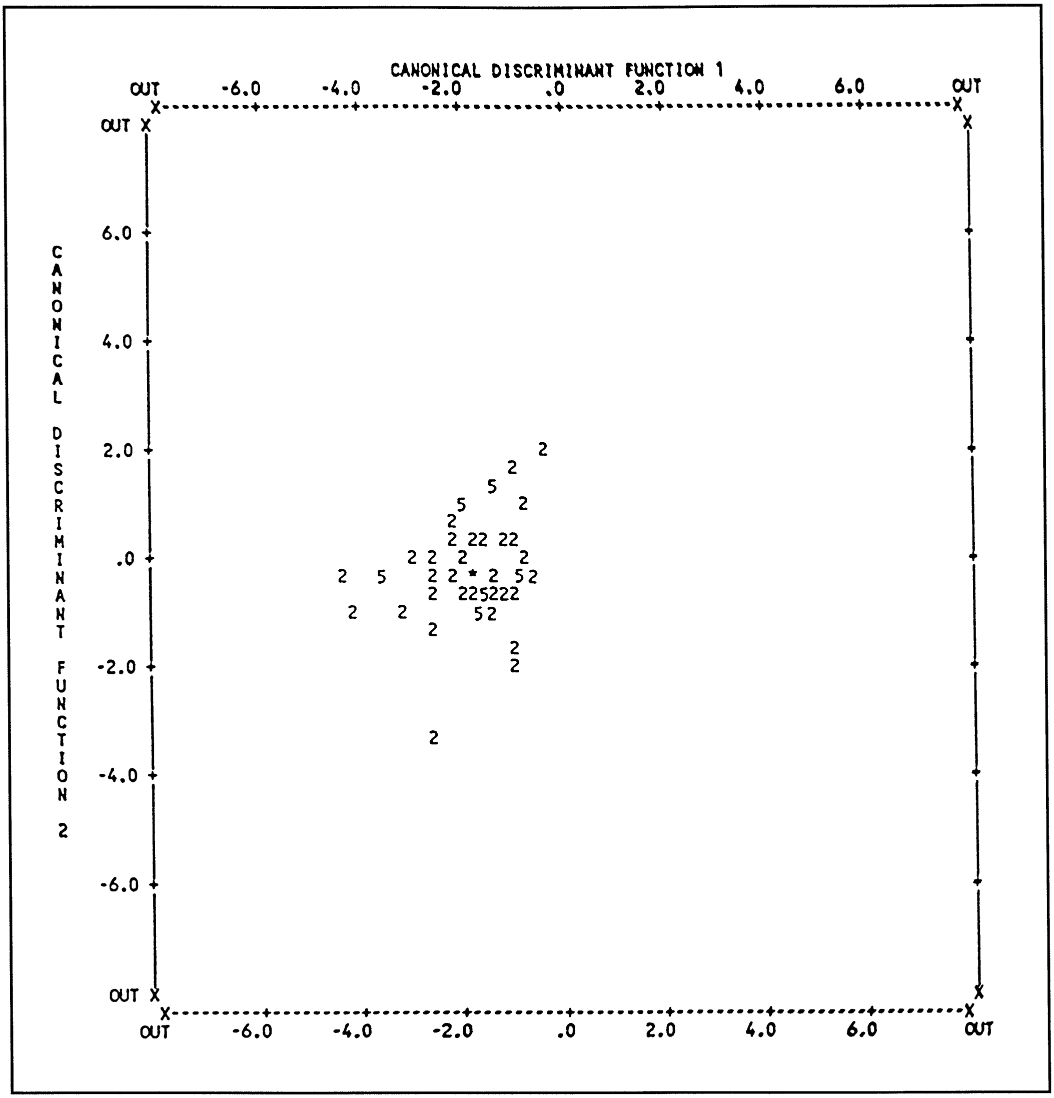

Fig. 9. Scatter plot for *P. leucopus*. Values are canonical variates, *P. leucopus* of Portage County, Wisconsin, comprising group 2. The six 5s were tentatively identified as *P. leucopus* from Washington Island, and this grouping confirms the identity.

Table 1. Mean lengths ± standard deviation of *Peromyscus* specimens from Wisconsin and Michigan

Group	*Locality*	*Ear*[1]	*Rostrum*[2]	*Tail*[3]	*Skull*[4]	*Incisive foramina*[5]	*Cranial width*[6]	*Rostral width*[7]
1	Lake Michigan Isles	18.85 ± 1.8	9.14 ± .42	83.13 ± 4.6	26.59 ± .52	5.15 ± .41	12.32 ± .43	4.54 ± .16
2	Central Wisconsin*	15.23 ± .93	8.32 ± .44	74.0 ± 7.0	25.96 ± .75	4.86 ± .4	——	4.60 ± .2
3	Lake Superior	16.96 ± 2.1	8.85 ± .43	83.6 ± 5.4	25.78 ± .73	5.20 ± .28	11.95 ± .24	4.29 ± .3

* (Portage County) *leucopus*

[1] N = 78, 42, 25 [2] N = 96, 35, 39 [3] N = 77, 42, 25 [4] N = 95, 35, 38 [5] N = 97, 36, 37 [6] N = 22, 13 [7] N = 18, 20, 14

Table 2. Analysis of variance of five measurements of *Peromyscus* spp.

	Linear measurement	*F*
1.	ear	53.37*
2.	rostrum	40.69*
3.	tail	33.02*
4.	total skull	13.60*
5.	incisive foramina	9.47*

* significant at $p < 0.05$

Acknowledgments

We wish to thank Drs. David Hillier and T. A. Neuhauser for helping with the computing. John Yost helped C. A. Long arrange specimens of deer mice. The University of Wisconsin–Stevens Point supported C. A. Long's sabbatical leave enjoyed at St. Olaf College. Dr. Eric M. Anderson and Adrian Wydeven gave appreciated advice on revising the manuscript.

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Table 3. Fisher's Linear Discriminant Functions. These classification coefficients may be applied to other samples.

	Lake Michigan Isles	*Central Wisconsin*	*Lake Superior*
Tail	0.640	0.483	0.766
Ear	1.340	0.310	0.459
Skull	72.225	73.331	71.062
Rostrum	-15.797	-20.279	-16.733
Incisive foramina	-0.019	0.188	1.965
Constants	-928	-889	-894

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Charles A. Long *is Professor of Biology and Museum Curator of Mammals at the University of Wisconsin–Stevens Point.*

John E. Long *is a graduate student in the School of Mathematics, University of Minnesota. C. Long was a Visiting Professor and J. Long a math major at St. Olaf College when the statistical study was initiated.*

John Lyons

Status and biology of Paddlefish (Polyodon spathula) *in the Lower Wisconsin River*

Abstract *The paddlefish* (Polyodon spathula) *is a Threatened Species in Wisconsin. Historically, paddlefish occurred over 224 km of the Lower Wisconsin River, from its mouth at the Mississippi River upstream to Wisconsin Dells. Paddlefish have not been reported from the 76 km between Wisconsin Dells and the Prairie du Sac Dam since the 1950s. A large population, possibly the largest remaining in Wisconsin, exists below the Prairie du Sac Dam, but further downstream, paddlefish are uncommon. From 1988 through 1990, several thousand paddlefish occurred in the 6-km stretch below the Prairie du Sac Dam. Paddlefish were most abundant in the 20-ha tailwater pool below the dam. Almost all paddlefish observed below the dam were large, with mean sizes of 15 kg and 134 cm total length, and maxima of 29.5 kg and 168 cm. Mean total length increased from 127 cm in 1988 to 139 cm in 1990. No young-of-year paddlefish and only one paddlefish under 5 kg were among the 237 paddlefish captured and weighed. The scarcity of small fish may have been merely a sampling bias or the result of poor spawning success and recruitment during the mid to late 1980s. Most paddlefish had evidence of recent parasitism by silver lampreys* (Ichthyomyzon unicuspis), *but lampreys probably did not cause substantial paddlefish mortality. Collisions with boats and snagging by anglers had injured many paddlefish. I recommend that management of paddlefish in the Lower Wisconsin River focus on: 1) improved understanding of reproduction and recruitment; 2) maintenance of a natural river flow regime; 3) continued prevention of illegal harvest; 4) re-establishment of a population above the Prairie du Sac Dam.*

The paddlefish (*Polyodon spathula)*, one of the largest and most unusual of Wisconsin fishes, was once much more widespread and abundant in Wisconsin than it is today (Becker 1983; Gengerke 1986). Before the beginning of intensive European settlement of the state 150 years ago, paddlefish were common in the Mississippi River and the lower reaches of its major tributary basins, the St. Croix, Chippewa, and Wisconsin. Small populations were also present in Lakes Michigan and Superior. Over the last 150 years, paddlefish have become far less abundant, disappearing from the Great Lakes by the early 1900s, and declining greatly in the Mississippi and its tributaries. Declines of paddlefish populations in Wisconsin and elsewhere have been attributed to habitat degradation, dam construction, water pollution, and possibly overharvest (Becker 1983; Pasch and Alexander 1986; Sparrowe 1986; Unkenholz 1986). The paddlefish is a Threatened Species in Wisconsin.

Paddlefish persist at only a few locations in Wisconsin (Becker 1983; Fago 1992). What may be the largest population occurs below the Prairie du Sac Dam on the Lower Wisconsin River in southwestern Wisconsin. Since 1988, I have studied the paddlefish below the dam, with the goal of collecting basic biological information necessary for preserving and increasing the population. In this paper, I report on the distribution and population status of paddlefish in the Lower Wisconsin River, and provide recommendations for managing the population. The data I present may serve as a baseline against which to judge future efforts to rehabilitate paddlefish populations throughout the state.

Study Area

The Wisconsin River originates at Lac Vieux Desert on the Wisconsin-Michigan boundary and flows 684 km south and west to the Mississippi River (Fig. 1). Since creation of the Lower Wisconsin State Riverway in 1989, the Lower Wisconsin River has usually been defined as the 148-km segment between the Mississippi River and the Prairie du Sac Dam, the first dam encountered upstream from the mouth of the Wisconsin (WDNR 1988). However, for purposes of this paper, I also include in my discussion of the Lower Wisconsin River the 76-km segment from the Prairie du Sac Dam upstream to the next dam, the Kilbourn Dam (river kilometer [RKM] 224) at Wisconsin Dells (Fig. 1). Historically, the biota of this segment were similar to those of the segment downstream from the Prairie du Sac Dam.

The Prairie du Sac Dam and the Kilbourn Dam are used for hydroelectric power. They are both impassable to fish moving upstream, although fish may be able to move downstream through them. The Prairie du Sac Dam has a head of 12.5 m and was constructed during 1911–1914, and the Kilbourn Dam has a head of 7.9 m and was constructed during 1907–1910 (Wisconsin Power and Light Corporation [WPLC], unpublished data). Presently, both dams are operated on a "run-of-the-river" basis, and water discharges through them are not regulated to any great extent. Dams further upstream on the Wisconsin River regulate river flows much more, and discharge patterns from these upstream dams can influence discharge patterns through the Kilbourn and Prairie du Sac dams.

The Lower Wisconsin River had mean annual discharges of 192 m^3/sec at the Kilbourn Dam in 1934–1990 (Holmstrom and Erickson 1990), 224 m^3/sec at the Prairie du Sac Dam in 1950-1989 (WPLC, unpublished data), and 246 m^3/sec at the Muscoda gaging station (RKM 71) in 1913–1990 (Holmstrom and Erickson 1990). Downstream from the Prairie du Sac Dam, the river is generally wide (> 200 m) and relatively shallow (< 3 m), with a primarily shifting sand bottom. Unique conditions exist immediately below the Prairie du Sac

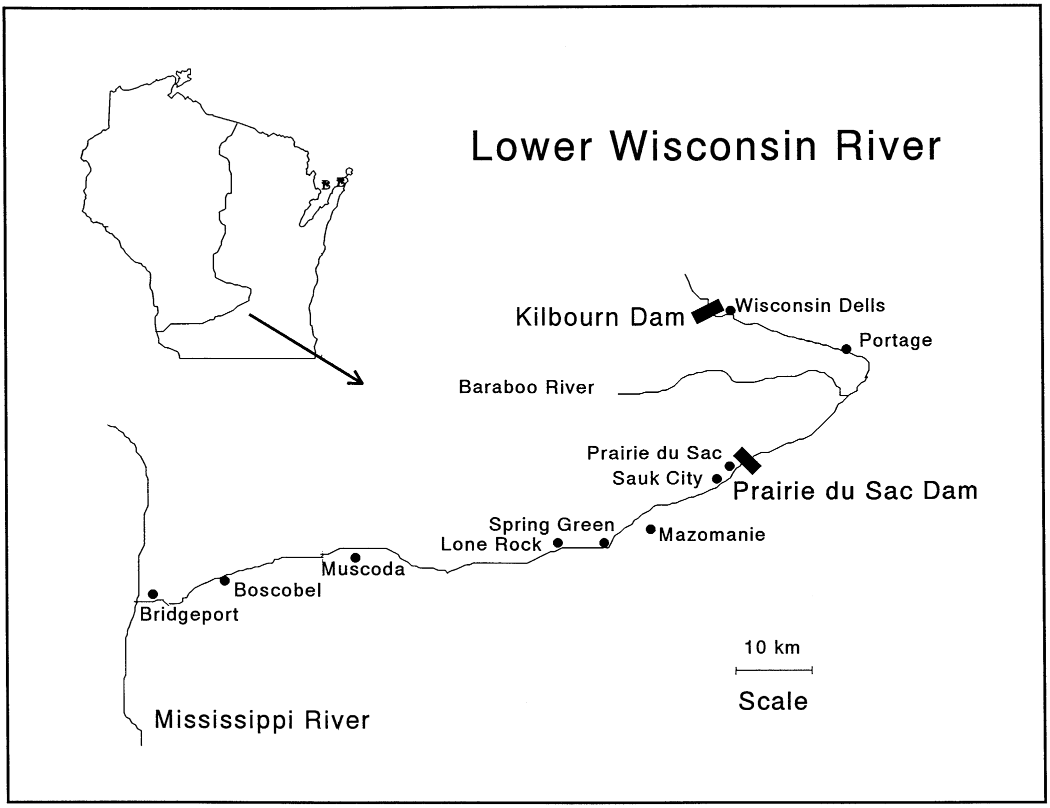

Fig. 1. Map of the Lower Wisconsin River, showing locations mentioned in the text.

Dam, where scouring has created a 20-ha tailwater pool that is over 12 m deep in places. The bottom in and adjacent to this pool contains relatively large amounts of gravel and cobble, although sand still predominates.

Methods

I obtained historical distribution and abundance data on paddlefish in the Lower Wisconsin River from published accounts, the Wisconsin Department of Natural Resources (WDNR) Fish Distribution Survey Database (Fago 1988), and unpublished records associated with paddlefish specimens preserved at the University of Wisconsin Zoological Museum (UWZM) in Madison and the University of Wisconsin Museum of Natural History (UWSP) in Stevens Point.

Current distribution and abundance data came from recent WDNR electroshocking surveys of the Lower Wisconsin River. The electroshockers used were standard WDNR two- or three-person, boat-mounted, pulsed direct-current "boom shockers," powered by either a 2500 watt or 5000 watt generator (Novotny and Priegel 1974). Between March and November 1985–1990, one to ten surveys per year were conducted in the area immediately below the Prairie du Sac Dam. Many paddlefish were observed during all of these surveys, but paddlefish were collected only from 1988 to 1990. Additional electroshocking surveys were conducted at sites closer to the Mississippi River on one date each in July 1985, April 1987, and June 1991, and on eight dates in October 1989.

During electroshocking surveys, efforts were made to minimize mortality of captured paddlefish. Paddlefish stunned by the electroshocker were quickly removed from the river and placed in a horse trough filled with river water. There they were measured to the nearest cm, weighed to the nearest 0.5 kg, checked for physical damage and lamprey parasitism, and then allowed to recover before being released. Normally, only one paddlefish was captured and processed at a time, and each captured fish was handled as little and as gently as possible. Most fish recovered from the electric shock within minutes, swam away strongly when released, and, presumably, survived. However, in each survey, some paddlefish (5 to 15%) died as a result of capture and handling. I took tissue and organ samples from 10 of the paddlefish that died between late March and early June 1990, and provided these samples for use in a nationwide paddlefish genetics study (Epifanio et al. 1990). I also examined stomach contents from these 10 paddlefish.

In previous studies, paddlefish size has been characterized by different length measurements (Russell 1986). To allow Lower Wisconsin River data to be compared with results from these earlier studies, four length measurements were made on most paddlefish captured: body length—the distance from the anterior edge of the eye to the caudal fork; mouth-fork length—the distance from the anterior tip of the jaw to the caudal fork; rostrum-fork length—the distance from the tip of the rostrum (paddle) to the caudal fork; and total length—the distance from the tip of the rostrum to the posterior tip of the upper caudal lobe. I used linear regression (SAS 1988) to develop equations to convert one measurement to another. I also used linear regression to develop quantitative length-weight relationships. I compared paddlefish total length distributions among different sampling periods with the Kruskal-Wallis test (SAS 1988). I estimated the approximate age of Wisconsin River paddlefish based on the total length-age relationship developed for paddlefish in Pool 13 of the Mississippi River (Gengerke 1978). I did not determine age directly because paddlefish must killed to be aged (Russell 1986).

In October of 1988 and 1989, I made mark-recapture estimates of the number of paddlefish in the area below the Prairie du Sac Dam. For two days each year, captured paddlefish were marked with a length of brightly colored plastic flagging tape that was wrapped around the caudal peduncle (13 in 1988; 29 in 1989). Within 48 hours of marking, the sampling crew made up to four electroshocking recapture passes in the vicinity of the dam, counting, but not netting, all paddlefish that surfaced between the electrodes (770 in 1988; 471 in 1989), and noting whether any of these paddlefish were marked (2 in 1988; 2 in 1989). The bright flagging tape was easily seen on paddlefish in the water. I estimated population size using the modified Petersen formula, with asymmetric confidence intervals calculated under the assumption that recapture probabilities for marked fish followed a Poisson distribution (Ricker 1975).

In 1989, I began an annual paddlefish abundance monitoring program. I established a standardized electroshocking circuit for paddlefish around the tailwater pool below the Prairie du Sac Dam. The circuit was about 1.6 km long and took up to 25 minutes to shock. In October 1989 and October 1990, the field crew shocked this circuit, counting, but not netting, all paddlefish observed, and noting whether each one appeared to be more or less than 100 cm in total length (a length at which paddlefish weigh approximately 5 kg). I used the total number observed in each circuit as an index of paddlefish abundance.

Historical Distribution and Abundance

The first reports of paddlefish from the Lower Wisconsin River date from the early 1900s, the period when the first scientific surveys of the fishes of the Wisconsin River were undertaken. Greene (1935), Becker (1966, 1983), and Fago (1992) summarized these surveys, and recorded paddlefish from the Wisconsin River at Prairie du Sac in 1924 and 1937 and at Wisconsin Dells in 1931. Wisconsin Dells probably was the historic upstream limit for paddlefish in the Wisconsin River. No paddlefish have ever been reported upstream from this point. Before completion of the Kilbourn Dam in 1910, a large rapids occurred in the Wisconsin Dells gorge (Stark 1988), and this rapids may have been impassable to paddlefish. Between the mid 1800s and 1910, a low-head (2 to 3 m), wooden logging dam was also present at Wisconsin Dells (Stark 1988), further impeding paddlefish upstream movement.

The last record of paddlefish from the stretch between the Prairie du Sac Dam and Wisconsin Dells came in 1950 (Becker 1983), when a large individual was found in the Baraboo River, a tributary that enters the Wisconsin River at RKM 181, near the city of Portage (Fig. 1). Fish surveys of this stretch of the Wisconsin River during the 1970s, 1980s, and 1990s failed to find paddlefish (Tim Larson, WDNR Fish Manager, Poynette, personal communication; David Morrow, fisheries biologist, Mead and Hunt, Inc., personal communication; personal observations). Causes of the disappearance of paddlefish are unknown, although I speculate that poor water quality in the river from the 1940s through the 1970s may have played a role. During this period, discharges from upstream industries, particularly paper mills, caused major declines in dissolved oxygen levels and were responsible for several large fish kills in the Lower Wisconsin River (Poff and Threinen 1965; WDNR 1976; WDNR, unpublished data). By the late 1970s, pollution abatement had greatly reduced water quality problems in the Lower Wisconsin River, but by then paddlefish were gone. The Prairie du Sac Dam prevents paddlefish from moving upstream and recolonizing this stretch of river.

Only eight confirmed records of paddlefish, all large individuals, exist from the Lower Wisconsin River below Sauk City (RKM 142) (Becker 1966, 1983; Fago 1992; UWSP Specimens; WDNR Fish Distribution Survey Database). Two records were from the early 1960s, when two dead paddlefish were found near Muscoda. The remaining six records were from extensive electroshocking and netting surveys that were carried out during the 1970s. One of these records (one fish) was from near the mouth of the Wisconsin at Bridgeport (RKM 10), and the other five (eight fish total) were from between Spring Green and Mazomanie (RKM 108 to 135) (Fig. 1). During these same 1970s surveys, over 125 paddlefish were captured from the 6 km of river between Sauk City and the Prairie du Sac Dam. In the 1980s, more than 2000 paddlefish were captured or observed in 38 days of electroshocking in the three kilometers immediately below the dam. Conversely, no paddlefish were observed in 11 days of shocking areas further downstream—one day upstream of Mazomanie (RKM 136–

142), one day near Lone Rock (RKM 95), and nine days from near the mouth up to Boscobel (RKM 3 to 45) (Fig. 1).

Paddlefish have been common in the area below the Prairie du Sac Dam for at least the last 50 years. During March 1945, "over a ton" of dead paddlefish was observed at Sauk City, presumably killed by poor water quality (UWZM, unpublished data). During the 1960s, large numbers of paddlefish were regularly observed directly below the powerhouse of the Prairie du Sac Dam (Poff and Threinen 1965; Becker 1966; UWZM, unpublished data; Lyle Christenson, WDNR Fisheries Research Biologist, Monona, personal communication).

From 1985 through 1990, numbers of paddlefish observed during surveys below the Prairie du Sac dam were typically 10 to 30 times higher in and adjacent to the tailwater pool than in areas further downstream. However, groups of 10 to 20 paddlefish were sometimes observed downstream from the tailwater pool, usually in the vicinity of the State Highway 60 Bridge in Prairie du Sac (RKM 146) or the railroad bridge in Sauk City (RKM 142).

Recent electroshocking surveys and discussions with anglers and scuba divers indicated that large numbers of paddlefish were present in the tailwater pool in all months of the year. At least 75 paddlefish were observed during each monthly electroshocking survey of the tailwater pool between March and November 1989. Anglers who fished the pool reported observing or accidently snagging paddlefish during all months of the year. In February 1982, scuba divers in the pool observed numerous large paddlefish (Mike Talbot, WDNR Fisheries Management Biologist, Madison, personal communication).

Although data are limited, there is no evidence that large numbers of paddlefish migrate to or from the area immediately below the dam. There are few confirmed records of paddlefish from the Lower Wisconsin River below the Prairie du Sac Dam or from Pool 10 of the Mississippi River at the mouth of the Wisconsin River (Becker 1966, 1983; WDNR Fish Distribution Survey Database), although a few commercial fishermen say that they regularly catch paddlefish in Pool 10 (Cecil Jennings, U.S. Fish and Wildlife Service Fisheries Biologist, LaCrosse, Wisconsin, personal communication). Moreover, genetic differences exist between the Prairie du Sac Dam paddlefish population and Mississippi River paddlefish populations (Epifanio et al. 1990), suggesting little mixing between paddlefish from the Wisconsin and Mississippi rivers.

The tailwater pool area of the Prairie du Sac Dam appears to have all the necessary habitats for paddlefish to complete their life cycle. Although paddlefish have not been observed spawning in Wisconsin waters, the gravel bars immediately below the tailwater pool conform to descriptions of good paddlefish spawning habitat (Purkett 1961; Pasch et al. 1980; Russell 1986; Crance 1987). The deep, slow-moving waters of the tailwater pool itself appear to constitute excellent summer feeding and winter resting habitat for both juveniles and adults (based on descriptions in Southall and Hubert 1984; Russell 1986; Crance 1987), and the lentic environment above the dam provides a source of crustacean zooplankton (personal observations), a primary food of paddlefish (Rosen and Hales 1981).

Abundance and Size Structure Below the Prairie du Sac Dam

During the late 1980s, several thousand paddlefish lived in the Prairie du Sac Dam tailwater pool. In October 1988, the estimated population size was 3600 (95% confidence interval: 1320–9000), and in October 1989 it was 4720 (95% confidence interval: 1730–11800). These may be overestimates, because only two marked paddlefish were recaptured in each month. Mark-recapture population estimates based on less than three recaptures tend to be biased, typically yielding estimates that are too high (Ricker 1975). Nonetheless, a population of several thousand paddlefish seems reasonable. Throughout the study period, it was normal to observe hundreds of paddlefish during two or three hours of shocking the tailwater pool.

No population estimate was made in 1990, but the abundance of paddlefish may have been less than in 1988 and 1989. The number observed along the standardized electroshocking circuit was 133 in 1989 and 78 in 1990. Generally, fewer paddlefish were observed during 1990 surveys than during 1988 and 1989 surveys.

Almost all of the paddlefish observed or captured were large. Of 237 paddlefish weighed, only one was less than 5 kg (4 kg; 97 cm total length [TL]). Of the hundreds of other paddlefish observed but not netted, only four appeared to weigh less than 5 kg. The mean size of captured paddlefish was 15 kg and 134 cm TL, and the maximum size was 29.5 kg and 168 cm TL (36 paddlefish with damaged upper caudal lobes or rostrums were not included in total length statistics). Nineteen percent of the captured paddlefish weighed 20 kg or more.

Based on the distribution of total lengths, most paddlefish were probably 8 to 14 years old, with the smallest individuals aged 4 to 7 years and the largest individuals greater than age 18 (Table 1). By age 8 to 12, all male paddlefish and most female paddlefish are likely to be mature (Gengerke 1978; Russell 1986), hence mature adults dominated catches in the Lower Wisconsin River from 1988 through 1990.

The average total length of captured paddlefish increased from 1988 to 1990 (Table 1). Over the period October 1988 through April 1989, paddlefish mean TL was 127 cm (I assumed no growth occurred between October and April). By October 1990, mean TL was significantly greater at 139 cm (chi-square = 28.7; p = 0.0001). During the period October 1988 through April 1989, 36% of captured paddlefish were less than 125 cm TL, and only 2% were greater than 145 cm. From October 1989 through April 1990, 14% were less than 125 cm and 34% were greater than 145 cm. By October 1990, only 3% were less than 125 cm and 38% were greater than 145 cm.

Sampling bias might account for the near absence of small paddlefish in electroshocking catches. In other river systems, young-of-year paddlefish have usually proven more difficult to capture than larger individuals (Purkett 1961; Pasch et al. 1980; Russell 1986). Boom shockers effectively sample only the top 2 m of the water column, and if small paddlefish occupy deeper water, they would not be vulnerable to capture. However, little is known about habitat use by small paddlefish (Russell 1986). Small paddlefish might occupy some other part of the Lower Wisconsin River and only move into the area below the Prairie du Sac Dam after they grow to a relatively large size. Although small paddlefish have never been captured in surveys of the Lower Wisconsin River outside of the Prairie du Sac Dam area, many kilometers of the river remain unsampled.

Conversely, the scarcity of small paddlefish in electroshocking samples might represent a real scarcity in the Lower Wisconsin River population. The increasing aver-

Table 1. Numbers of paddlefish captured, by total length (TL) class, from below the Prairie du Sac Dam, Lower Wisconsin River, 1988–1990. Only fish without damaged rostrums or upper caudal lobes are included. Paddlefish captured between October and April are combined because I assumed that no growth occurred during this time interval. Approximate age ranges are based on data from Mississippi River paddlefish (Gengerke 1978).

		October through April Only			
TL Class (cm)	*All Months, Years Combined*	*88–89*	*89–90*	*90–91*[a]	*Age Range*
<100	1	1	0	0	4–7
100–104	0	0	0	0	4–7
105–109	1	0	0	0	5–7
110–114	6	2	1	0	6–9
115–119	10	3	4	1	7–10
120–124	23	10	3	0	8–12
125–129	36	13	4	6	8–12
130–134	29	6	7	6	9–13
135–139	34	7	10	4	9–14
140–144	18	2	8	1	12–18
145–149	19	0	6	5	14–18
150–154	14	0	6	3	16–18
155–159	8	1	4	1	≥18
160–164	4	0	2	2	≥18
165–169	1	0	1	0	>18
Totals	204	45	56	29	
Mean TL	134	127	139	139	
Standard Deviation	12.1	9.5	12.6	11.0	

[a] High flows prevented effective sampling for paddlefish in March & April 1991.

age lengths of captured paddlefish suggest that there was little recruitment to the adult population during the study period. Poor reproductive success during the mid to late 1980s could explain the low numbers of young paddlefish.

The time of paddlefish spawning in Wisconsin waters is unknown (Becker 1983), but based on preferred water temperatures for reproduction (15 to 22°C), and the spawning season in states to the south (mid to late April in Missouri and Tennessee—Purkett 1961; Pasch et al. 1980; late April to late May in Iowa—Southall and Hubert 1984), paddlefish in the Lower Wisconsin River probably spawn in May. Water temperatures below the Prairie du Sac Dam range from 11 to 17°C in early May and 18 to 22°C in late May (Don Fago, WDNR Fisheries Research Biologist, Fitchburg, unpublished data for 1987–1990). Paddlefish reproductive success tends to be highest in years when river flows are at or near flood levels during and for at least a week after spawning (Purkett 1961; Russell 1986). The specific flows required to provide good spawning conditions at a site depend on the morphometry of the river channel; paddlefish normally spawn on submerged gravel bars with water velocities greater than 0.4 m/sec and depths greater than 2 m (Crance 1987). Thus, river flows in May probably determine paddlefish reproductive success in the Lower Wisconsin River.

I hypothesize that river flows in May at the Prairie du Sac Dam might have been below the optimum for paddlefish reproduction during most of the 1980s. Based on my extensive observations of the Lower Wisconsin River over a wide range of flows and an examination of the discharge vs. water level relationship below the dam, I have found that large areas of submerged gravel bars with depths deeper than 2 m and water velocities greater than 0.4 m/sec occur in the vicinity of the dam only when river flows are greater than 400 m^3/sec. Mean flow in May at the Prairie du Sac Dam was 306 m^3/sec in 1950–1990 (WPLC, unpublished data). Since 1950, flows in May have exceeded 400 m^3/sec for more than seven consecutive days (and hence been best for paddlefish spawning) in nine years: 1951, 1954, 1960, 1965, 1972, 1973, 1975, 1979, and 1984 (WPLC, unpublished data). Thus, flows likely to produce optimal spawning conditions occurred only once during the 1980s. Seven of the years in the 1980s had mean May flows below the long-term average. The 8- to 18-year-old paddlefish that dominated catches in 1988–1990 were hatched between 1970 and 1982, a period in which four years of optimal flows occurred.

Miscellaneous Observations

The four length measurements made on paddlefish from the Lower Wisconsin River were strongly correlated with each other. Regressions relating each measurement to total length and body length, the most common measurements in the literature, are as follows:

Total Length = 20.384 + (1.271 x Body Length)
(N = 202; F = 1639; p = 0.0001; r^2 = 0.89)

Total Length = 22.231 + (1.242 x Mouth-Fork Length)
(N = 203; F = 1760; p = 0.0001; r^2 = 0.90)

Total Length = 3.421 + (1.074 x Rostrum-Fork Length)
(N = 203; F =3294; p = 0.0001; r^2 = 0.94)

Body Length = 2.747 + (0.963 x Mouth-Fork Length)
(N = 217; F = 10106; p = 0.0001; r^2 = 0.98)

Body Length = -6.480 + (0.789 x Rostrum-Fork Length)
(N = 205; F = 2537; p = 0.0001; r^2 = 0.93)

Paddlefish weight was also strongly correlated with both total length and body length:

Log_e(Weight) = -12.706 + (3.132 x Log_e [Total Length])
(N = 202; F = 484; p = 0.0001; r^2 = 0.71)

Log_e(Weight) = -10.408 + (2.902 x Log_e [Body Length])
(N = 213; F = 686; p = 0.0001; r^2 = 0.76)

Nearly all paddlefish from below the Prairie du Sac Dam suffered from parasitism by silver lampreys *(Ichthyomyzon unicuspis)*. Of 240 paddlefish examined, 231 (96%) had either an attached lamprey or a fresh lamprey wound. Individual paddlefish had up to 11 attached lampreys and 28 fresh wounds; the mean number of lampreys attached was 1.2 and the mean number of fresh wounds was 6.1. Most paddlefish also had healed wounds from previous lamprey attacks.

I do not believe that lampreys cause substantial mortality of paddlefish in the Lower Wisconsin River. Lamprey parasitism has been common on Lower Wisconsin River paddlefish since at least the 1940s (UWZM, unpublished data), and yet a large paddlefish population persists. The prevalence of healed wounds on paddlefish shows that paddlefish survive lamprey attacks. The ratio of paddlefish biomass to attached lamprey biomass is typically much more than

50 to 1. In experiments involving sea lampreys (*Petromyzon marinus)* feeding on lake trout *(Salvelinus namaycush*) and rainbow trout (*Oncorhynchus mykiss*), Farmer et al. (1975) found that lampreys caused direct mortality of their host only when the ratio of host biomass to lamprey biomass was less than 40 to 1.

Some paddlefish had injuries or tissue damage not caused by lampreys. Twelve of 240 paddlefish (5%) had damaged rostrums, and 55 (23%) had external damage to some other part of the body. In some instances paddlefish had lost most or all of their rostrum. Much of the damage clearly had been caused by fishing hooks and lines or by boat motor propellers. Paddlefish often swam just below the surface, and on several occasions I saw motor boats collide with them. Although fishing for paddlefish is illegal, I sometimes saw anglers deliberately trying to snag them. When anglers did catch paddlefish, they would often handle them roughly and keep them out of the water for long periods.

The frequency of tissue damage for paddlefish from below the Prairie du Sac Dam was similar to that observed elsewhere. In Pool 13 of the Mississippi River, Gengerke (1978) reported that 30 (5%) of 603 paddlefish had damaged rostrums. However, only 91 of 1543 paddlefish (6%) had damage from fishing hooks and lines or boat propellers. In the Missouri River in South Dakota, 46 of 458 paddlefish (10%) had damaged rostrums, and an additional 118 (26%) had damage to other parts of their body (Rosen and Hales 1980). Most of this damage was attributed to fishing hooks and lines or to boat propellers.

Paddlefish appeared to travel in schools below the Prairie du Sac Dam. Paddlefish were usually observed in groups of 10 or more. It was common to electroshock an area of the tailwater pool and observe no paddlefish, only to return several hours later and observe many paddlefish. However, paddlefish distribution in the tailwater pool was not random. Certain areas, particularly eddies adjacent to fast current, consistently had higher numbers of paddlefish than elsewhere.

Based on limited data, it appeared that paddlefish from below the Prairie du Sac Dam fed largely on crustacean zooplankton. All 10 of the paddlefish stomachs examined between late March and early May 1990 contained primarily *Daphnia*, a crustacean zooplankter that was present in high densities in the tailwater pool during this period (personal observations). The amount of food in the stomachs was impressive; several contained more than 1 kg (wet weight) of *Daphnia.* Other studies have reported that crustacean zooplankton are a major food of paddlefish (Wagner 1908; Rosen and Hales 1981; Becker 1983; Russell 1986).

Management Recommendations

I believe that a priority in management of the paddlefish population of the Lower Wisconsin River should be to learn more about the distribution and abundance of small (i.e., < 5 kg) paddlefish. Until the reason for the scarcity of small paddlefish in electroshocking samples can be explained, management efforts will be hampered by uncertainty about the size and abundance trends of the population. I recommend a two-part study to clarify the status of small paddlefish. The first part should determine whether electroshocking is biased towards larger paddlefish. A variety of methods that effectively sample deep water, such as trammel and gill netting, seining, and trawling, should be compared with electroshocking in the tailwater pool and in areas further downstream. If these other techniques capture small paddlefish in good numbers, then they should be used together with electroshocking in the annual abundance monitoring program.

The second part of the study should determine where, when, and under what conditions paddlefish reproduce successfully in the Lower Wisconsin River. Efforts to preserve and increase the paddlefish population below the Prairie du Sac Dam would be enhanced by a better understanding of factors that dictate spawning success and subsequent recruitment to the adult population. Because optimal conditions for paddlefish spawning might occur only a few times each decade, this part of the study could take many years to complete.

The likelihood that paddlefish need high river flows for successful spawning suggests that paddlefish reproduction might be enhanced if the Prairie du Sac Dam and upstream dams artificially increased flows during May. However, I recommend against this for several reasons. First, there are no actual data on paddlefish spawning in the Lower Wisconsin River. As a result, it is impossible to provide precise recommendations as to when, how much, and for how long flows should be augmented. The river flow conditions that I have suggested were optimal for paddlefish reproduction represent a hypothesis that needs to be confirmed with field data before changes in dam operations are considered. Second, neither the Prairie du Sac Dam nor the Kilbourn Dam have substantial water storage capacity, and it is unlikely that they could be used to increase flows without unacceptable declines in the levels of the impoundments behind them. Moreover, the Prairie du Sac Dam is in the process of being licensed by the Federal Energy Regulatory Commission (FERC), and a condition of the license will be that the dam continue to operate in run-of-the-river mode. The WDNR will also recommend continued run-of-the-river operation of the Kilbourn Dam if it is licensed by FERC (Bob Hansis, WDNR Water Management Specialist, Fitchburg, personal communication). Several dams upstream from the Kilbourn Dam have large storage capacity, but using them to increase flows below the Prairie du Sac Dam would be complicated. Finally, although artificial high flows might benefit paddlefish, they might harm other species. The biotic community of the Lower Wisconsin River is complex, and modification of natural flow patterns, however well intentioned, might have unforeseen negative consequences. I recommend taking a conservative management tack and changing natural river flows as little as possible.

Illegal harvest is a threat to the paddlefish population in the Lower Wisconsin River. Paddlefish eggs make excellent caviar and fetch high prices. The potential to earn large amounts of money by selling paddlefish eggs has led to considerable organized illegal harvest in some areas, and caused serious harm to paddlefish populations in some waters (Missouri Department of Conservation and U.S. Fish and Wildlife Service, unpublished data). Although there is no evidence of substantial illegal harvest in the Lower Wisconsin River, the year-round concentration of paddlefish below the Prairie du Sac Dam makes the population vulnerable to illegal snagging and netting. The area below the dam is regularly patrolled by WDNR Law Enforcement personnel, but if evidence of substantial illegal harvest comes to light, the patrols should be increased.

Recreational use of the area below the Prairie du Sac Dam clearly causes injuries to many paddlefish, although the effect of these injuries on the paddlefish population is uncertain. Two actions could be taken to reduce the number of paddlefish injuries. First, the tailwater pool area could be declared a "no wake" zone. Boaters would be required to travel slowly when in the area, allowing them and the paddlefish more time to see each other and avoid collisions. Second, educational signs and pamphlets could be developed to urge anglers to avoid trying to snag paddlefish, and to release quickly and carefully any paddlefish they caught accidentally.

I recommend that an attempt be made to re-establish paddlefish in the stretch of river between the Prairie du Sac Dam and the Kilbourn Dam. Water quality in the area below the Kilbourn Dam has improved markedly since the 1960s and 1970s, and the habitat there appears to have depth, velocity, and substrate characteristics suitable for paddlefish. The best source of paddlefish for reintroduction would be from below the Prairie du Sac Dam. The paddlefish from here are probably part of the same stock that once inhabited the area below the Kilbourn Dam, and by using them, the potential for introducing genetically unsuitable fish would be minimized (Epifanio et al. 1990). The population of paddlefish below the Prairie du Sac Dam is large enough that removal of some individuals (< 250) for stocking upstream probably would not be harmful.

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John Lyons is a fisheries research biologist with the Wisconsin Department of Natural Resources. His research focuses on the ecology and management of fish in warmwater streams and rivers.

Bruce Taylor

An "Education into Gladness": Ron Wallace's The Makings of Happiness *and "The Mid-life Progress" narrative*

As Director of Creative Writing at the University of Wisconsin–Madison and Editor of the annual Bittingham Award for poetry from the University of Wisconsin Press, Ron Wallace, both as a practitioner and a promoter, has been for many years a major voice of and for poetry in Wisconsin. As author of three previous books of poetry, three books of criticism, and as editor of the anthology *Vital Signs: Contemporary American Poetry from the University Presses*, Wallace's national reputation has been firmly established for quite some time. However, with the publication of *The Makings of Happiness*, Wallace has emerged squarely among the very best of the mid-generation poets in America.

The Makings of Happiness is a book of broad appeal that can be enjoyed on many levels and from many different perspectives, a book for the general reader as well as the most seasoned poetry aficionado. An hour, an afternoon, a day, or many days can be spent wallowing in this book's sumptuous pleasures. The more a reader puts into it, the more he or she gets out of it—and that, after all, is the hallmark of great literature.

To even the casual reader of Ron Wallace's poems there is much wit and music to be found, great humor and many words at wonderful play. First, on this most available level, there is all the beautiful noise, all the language which delights the reader by delighting in itself.

I'm lifting the oysters
up from the ice chips,
scooping the slippery pap
loose with a spoon,
dripping the sliver of lemon, the ripe
island of tabasco, and then
flipping it all up to my lip and sipping
it in, the rough texture of shell
on incisor, the limp liquidy tongue
poised for the pleasure
of soft palate and swallow . . .
"Fresh Oysters & Beer"

Limp-wristed and slithery
she spins full around
and falls to the ground
dizzy, a fizzle.
"Wiffle Ball"

Breezy with bees
apple pulp rises under the grinder,
shreds of flesh and skin glistening,
the amber liquid dripping
into the tin acidic bucket.
"Apple Cider"

the tin stars pinned
in the tenpenny wind.
"February Thaw"

Even more simply, though no less elegantly, Wallace displays an impeccable diction, illuminating again how the difference between a word and the "right" word is, as Mark Twain has always told us, the difference between "lightning" and a "lightning-bug." Wallace gives us the "*rampantly* adolescent daughter" of "Fresh Oysters & Beer"; a "*puff* of nuthatch" and "roadside mud *quick* with rivulets" in "February Thaw"; in "Prayer," "the *wick* of your own breath *aflutter*," as well as the exquisitely assonantial

Or the votive candles of snow
over which one crow,
cowled in its shadow, lengthens?[1]

Then there is the deft ability Wallace has for reinventing the language with phrases to which he has restored original meaning by forcing them within the context of the poem back through the colloquialisms, clichés and euphemisms, the commonplaces of homely discourse to reassume their original power as metaphor. For example, in "Early Brass" the brass section of the New York Cornet & Sacbut Ensemble, "in long-tailed tuxedos / rise to the *bright occasion*." Marjorie, the quadriplegic "information manager of a chin operated wheelchair company," composes in "Fan Mail" a "chin-operated missive, / its five good-tempered sentences / tapped out with what *intensive care* . . . ."[2]

In "Basketball" the poet is shooting baskets with his six-year-old daughter who is dawdling:

Hurry up, I shout.
We don't have all day.
And we don't.
The next time I look,
she's sixteen . . .[3]

Wallace is capable of many wonderful lines and of many master-crafted individual poems. Yet, as enticing as it is to remain at this level, if the reader considers *The Makings of Happiness* merely as a collection and not as a progression with a beginning, middle and end, then that reader will miss the full scope and profundity of what, when read in sequence, reveals itself as a remarkable narrative—the slow, often sad, but ultimately miraculous story of many of us.

With this book meticulously arranged in three incremental sections, Wallace leads the reader through a progression of poems that ultimately achieves an equilibrium between richness and loss, regret and ease. Through the sequence of these wryly, often ironically bemused, superbly wrought poems, *Makings* shares much with the recent American fiction described by Margaret Morganroth Gullette in *Safe at Last in the Middle Years* as "mid-life progress narratives "(xiv). Gullette voices the recognition that "rescuing them [the protagonists/subjects] from . . . depletion seems to be one of the . . . unspoken spiritual or ethical functions" (xiv); and that these kinds of narratives utilize their "resistances, strengths, or sly timely weaknesses, ingenious mental feints" to achieve a resolution in which the author can begin even "to think the kind of sentence" that would have been impossible before (xiv.31). So, near the end of Wallace's book we find lines such as

> How ease inhabits our lives.
> "The Fox in the Berry Patch"

and in the same poem,

> . . . O the gladness
> that only a family understands . . .
> "The Fat of the Land"

Standing as they do above, out of context and in isolation, these lines could be dismissed as glib and self-serving by a less than attentive reader. But by the time the careful reader gets to these lines, and the poems they are part of, the poet has earned the right to such statements. Though what damns us saves us, and all that can save us from ourselves is time and change, here, according to Gullette, there is "no necessary contradiction between gladness and the self as it lives in time." Here then for both the poet and the reader is an enticement into hopefulness, or as Gullette calls it, an "education into gladness" (146).

> If a man can't be happy on a little farm
> in Wisconsin,
> he hasn't the makings of happiness in
> his soul.
> Nick Englebert, artist-farmer,
> 1881–1962

The conditional "if" of the title epigram, with which Wallace's book both begins and ends, raises the central question of the collection. The question is not, what is happiness, not exactly; but more, of what and how is happiness made? What, if you will, is the recipe? What are the ingredients?

Early Brass

The poems of the first section, "Early Brass," are both strident and timid, full of failures feared or perceived and all the initiatory anxieties of youth "duped by dazzle and subterfuge, / shimmer and flick" ("Bluegills") where "desire and longing could inspire / the unlikeliest situation" ("Love and Sex").[4]

Wallace seeks in the past (our memory, our *makings* of the past) some distant prophecy of what the future has become. The speaker, even in this first section, simultaneously assumes the voice of both child and father: the early awkward lover and practiced husband, the tentative young poet looking hopefully ahead and the master crafter looking back, however helplessly, towards the past which in its own way seems as mysterious now as the future did then.

Change and perspective are the major ingredients introduced in the first section, and time is the catalyst. The future from this "early" view seems always "somewhere overhead, . . . / stretched out filmy and seductive" ("Smoking"). The past, on the other hand, can be realized only in retrospect as "a vast doorway" ("Fan Mail"), ". . . one more / phantasmagoric invention we use / to fool ourselves into someone else's shoes" ("Off the Record").

In "Speeding":

> Some damn fool kid
> is racing his three-speed
> down the hill in front of our house
> . . .

and later,

> spring flashing its bright green signals,
> although, approaching fast from a
> side street,
> the future is looming,
> preparing to barrel through.
> *Look out! I* shout. But it's too late.
> The kid has been gone for years,
> pedaling for all he was worth
> into me, into you.

The events of these "early" poems, while they were happening, seemed to be all ". . . heading for the future / just as fast as the mind can see" ("Camp Calvary"); yet the same events seen in retrospect, the stance that the mature artist is allowed by the art itself, assume the slow motions of the inevitable, of ". . . the ball slowly / rolling out the door / and down these many years" ("Rebounding"). The difference in perspective is the result of the change time has brought to the poet, and the attempt to fix the events themselves within the artistic frame of the poems.

Breakdown

The second section of the book, "Breakdown," is one of crises and passages, accidents and escapes, close calls and catastrophes. The possibilities of luck and the fact of evil itself must at least be "gotten by," if not "gotten through."[5] Again, it is the meliorations of art that make such a passage possible.[6] If "Turning Forty" (the title of one of the poems) is "over the hill," then being "At Forty" (the title of another) is the hump; and once again it is the act of the poems, the learning of the *makings* of them, that allows the "getting over."[7]

"Breakdown," the title and first poem of this section, begins with that moment before a seemingly inescapable accident which, however, does not happen: "When you finally know / you are not going to make it," and ends with an escape, with ". . . nothing changed

> except for this small uncertainty,
> this fist in your gut, this sneer
> twisting your lips, as if
> you knew something true and awful,
> something you could never, never
> confess.

The accident which is ultimately avoided is middle-age with its intimations of mortality, its chances lost or not taken, with more doors closed behind than ever able to be opened ahead. As in the first section of this book, the initial motion seems to be forward, often out of control, as in "Hairpin":

> in the bright slow deceptions of the day,
> you race toward that sudden
> appointment
> you never quite planned on,
> the journey you didn't mean to take.

Or, in "Headlines":

> . . . morning careening just around the
> corner, your own spring flagging, the
> drought burning on?

Yet, there is also a pause here, a slow progression to the realization that we both lose and gain as we grow, that, as is noted in "Turning Forty":

> Time doesn't speed up like a train
> with somewhere to get to, railing
> on that Augustinian straight line,
>
> so much as it spirals, silent, circling
> back on itself, an old dog, settling
> on the same tired spot again . . .

and that there is a certain joy to all this when

> In the country of stumble and drag
> time settles, its bald tail a-wag.

In the first section of the book there were poems such as "Early Brass," "Rebounding," and, particularly, ""Birdsong Anyway" where the subject was the poet early at his art, the first few fumblings, the initial impulses which brought the poet to that art at all. In the second section, in poems such as the "Poetry Report," "State Poetry Day," and "The Dinner Party," it is the distractions of the pseudo-settled (the middle-aged, middle-class, and middle-brow), the temptations of the hack and the poetaster, that threaten the poet's progress towards the authentic.

In "State Poetry Day" (surely the most cacophonous villanelle ever written), poetry threatens not even to survive, as Auden once demurred, "in the valley of its saying," when, "In the legislative chambers with their dactyls and caesuras / the local poet laureates sing in praise of cheese and beer," and where

> No one mentions Nicaragua, acid rain,
> cocaine or Star Wars,
> as the couplets and quatrains maintain
> a pleasant atmosphere.
>
> The mayor couldn't be here, but he
> sends his grand whereases.
> Another year closes with a villanelle's
> razzmatazzes.

In the next poem, "The Dinner Party," a sestina, the poet, in another room, becomes aware that

> Everyone out in the living room's
> concerned
> about groundwater and nuclear war,
> their voices a warm glow in the dark,
> the familiar country of engaging
> party talk,
> and I'm here in the kitchen with
> my spinach
> and my eggs, my vinegar and oil,
> worrying
>
> about how to make a salad. . . .

It seems, then, no accident that these poems are followed by another pair, "The Hell Mural: Panel I" and "The Hell Mural: Panel II" which are also sestina and villanelle, that profoundly and majestically address those same subjects that the previous pair so trivially if artfully avoid. The poet moves from the light, almost parodic tone of the first pair to the high seriousness, the elegiac thunder of the second. (Both poems take as their subject The Hell Mural, impressions of the Hiroshima holocaust painted by Iri and Toshi Maruki.)

Thus this section of the book ends with two confrontations of an ultimate evil, each in the strictest of forms, as if those restrictions can contain the horror—the scope too large, the cast too numerous in its sufferings, the implications too gigantic to comprehend.

The Makings of Happiness

Is it escape then, that drives the poet to the "small farm in Wisconsin" of the Engelbert epigraph? Is it the world too much to handle, the realization of the impossibility of hanging on to anything except yourself and your own, to the few people that there is no doubt you belong to, and to a place, however imperfect, of your own making?

Yes, but not just. In this third and final section, the poet, full in the flourish of his talent, takes the way in to find the way out. He attempts, as poets almost always have, the ultimately universal through the deeply personal, struggling though the only life each of us has towards those other lives around us and toward the Life that surrounds and supports us all: the life of nature and the life of place, the life of family and work—which in this case is the poet at his craft.

The place is, of course, essential to this last section of the book. The farm, away from the bustle of the city and distractions of a larger society, allows the poet the time and space to focus and concentrate—quite literally, to see.

> Far from the city with its bright
> deceptions,
> we lie down in the damp grass and
> await whatever
> blast of heat or radiance is on its way
> to take us
> out of ourselves into the future that
> couldn't be.
> Tomorrow, the papers will claim
> aurora borealis,
> a rare display for those with dark
> enough to see.
> "Night in the Country"

The farmhouse itself, full of the immediate family, when viewed from the outside on a cold winter night, achieves the perspective of rebirth and renewal:

> . . . the warm house brightens
> as if the click of the refrigerator
> and the slow breathing of the children
> could call up the whippoorwill,
> cicada, spring peeper, and cricket,
> could fill us beyond loss or doubt.
> "February, Full Moon"

Family is key here. It is the "glue," if you will, that holds the place together. In "The Fat of the Land" it is the extended family gathered for a reunion primarily, it seems, to eat, to partake of, not just food, but of each other:

> . . . one big happy family, back from
> wherever we've spread ourselves too thin.
> A cornucopia of cousins and uncles,
> grand-
> parents and aunts, nieces and nephews,
> expanding.

and later,

> O the loveliness of so much loved flesh,
> the litany of split seams and puffed
> sleeves,
> sack dresses and Sansabelt slacks,
> dimpled knees and knuckles, the jiggle
> of triple chins. O the gladness
> that only a family understands . . .

and finally,

> . . . huge and whole of this
> simmering night,
> battened against the small skinny
> futures that must befall all of us,
> the gray thin days and the
> noncaloric dark.

Ultimately, however, it is the poet, and the poet's craft learned and practiced, that provides the last ingredient for Wallace's recipe for happiness: to love and enjoy the moment, the day, and the world, the people who are yours in it, and to do good work.

In the first section of the book, in "Birdsong Anyway," the young poet attempts the metaphor of poem as birdhouse and fails, at least at the constructing of the house itself. In the first poem of the third section, "Building an Outhouse," a wryly, nearly perfectly diswrought sonnet which is also about "building" poems, the poet can concluded with confidence:

> . . . it's up! Functional. Tight as
> a sonnet.
> It will last forever (or at least for awhile)
> though the critics come sit on it, and
> sit on it.

How else to get through the day and the life, both past and future, however tenuous, that this day is a part of, but to bring it to the poem and there allow the connections to be made between the aging, changing self and the family and place the self finds itself a part of. The poem, of course, cannot capture the moment, but can fix it and frame it, shape it into one of those, as Wordsworth called them, "spots in time," or in Frost's words, "momentary stays against the confusion," in which the self, glad in the present, experiences grace.

This is, however, a grace more Frost than Wordsworth, for it is a condition, though perhaps given, only available to the poet active and aroused at the makings of poetry. The classic metaphor of Walt Whitman also comes to mind here, of the "Noiseless Patient Spider," "isolated / Mark'd how to explore the vacant vast surrounding, / It launched forth filament, filament, filament, out of itself" compared to the Soul/Poet, "detached in measureless oceans of space, / Ceaselessly musing,

> venturing, throwing, seeking the spheres
> to connect them,
> Till the bridge you will need be form'd,
> till the ductile anchor hold,
> Till the gossamer thread you fling
> catch somewhere . . .

It is in the final, title poem, "The Makings of Happiness," that these connections are most obviously made. The poem is based upon a painting by Nick Englebert, "*The Photographer,*" which also provides the epigraph for this book. The literal subject of the painting, as the title implies, is not primarily a "small Wisconsin farm" but a visiting turn-of-the-century French photographer taking a picture of a Wisconsin farm family. This was an event at that time of great wonder, rarity and delight. The necessity of the role of the artist then is inherent in the progressive tense of the poem's, and book's, title, the "*Makings.*"

It is not, as the poem tells us, "Until you have looked at something so long / it grows so familiar you can't see it," that you can "know the soul's work." The expressive role of the artist here—painter, photographer and poet—is to reveal the miraculous in the daily, homely and commonplace,

> the alp that all but disappears in dailiness;
> the sea that common routine conceals;
> the little farm in Wisconsin that seems
> painted in oil on your long picture
> window . . .

and to create

> the barn more like a hearth than a barn,
> a mother, who could be your mother,
> in the doorframe across the way,
> bread in the oven and time on
> her hands,
> the little girl, who could be a boy,
> roped to her calf, which could be a dog,
> waving to her cat, which could be
> a stoat,
> apples in her cheeks and honey in
> her hair,
> the church in the permanent center,
> the townspeople happy as larks . . .

What is important to keep in mind are the layers of references the poem has established. It is not the farm or the family itself, not the photographer's picture of it and them, not even the painter's picture of the photographer taking his picture, but the poem of the poet that pulls it all together and keeps

> . . . the man floating, the girl
> smiling, the calf changing, the cow
> rolling
> its eyes, the blue Frenchman tipping
> his hat at you who live so far off
> in the vanishing point of the future.

Notes

[1] Italics in this paragraph are mine.

[2] Italics in this paragraph are mine.

[3] Italics are in the original.

[4] "To feel good about the middle years it is helpful to have had a miserable young adulthood . . ." Gullette observes, while later adding that from the advantage of the "later, . . . safer middle years, . . . young adults [are regarded] with detached sorrow, pity, and compassion—as if . . . we now understand how the young are obliged to navigate a perilous crossing with rudimentary equipment before getting to the other side" (6–7).

[5] "Suddenly we see what must be the basic psychological situation, and it's the same whether the plot trouble is sex or parents or children or war. Whatever it is, the characters fear that for some reason they don't understand, they can't create a self-chosen, more self-confident, happier future —they can't progress in the life course as they must and want to." For this reason, I believe, dangerous-age novels contain more than their share of shrieks, blows, accidents, and death" (Gullette 15).

[6] "Meliorism is the narrative message of mid-life *Bildungsromane*" (Gullette 150).

[7] "The ability to recognize that the middle years can be welcomed as a relief by some people may depend on our traversing the dangerous age imaginatively, in however truncated and inevitably detached a way" (Gullette 18–19).

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Poet and Editor ***Bruce Taylor*** *is Professor of English at the University of Wisconsin-Eau Claire. His most recent essays include "The Vietnam War Movie: Voyeur and Witness" and "Draft Dodger Rag" in* The Highground, *published by the Wisconsin Vietnam Memorial Project Inc., and "Betrayed and Abandoned: The Divorced Male in the Short Fiction of John Updike" in* Wisconsin Dialogue.