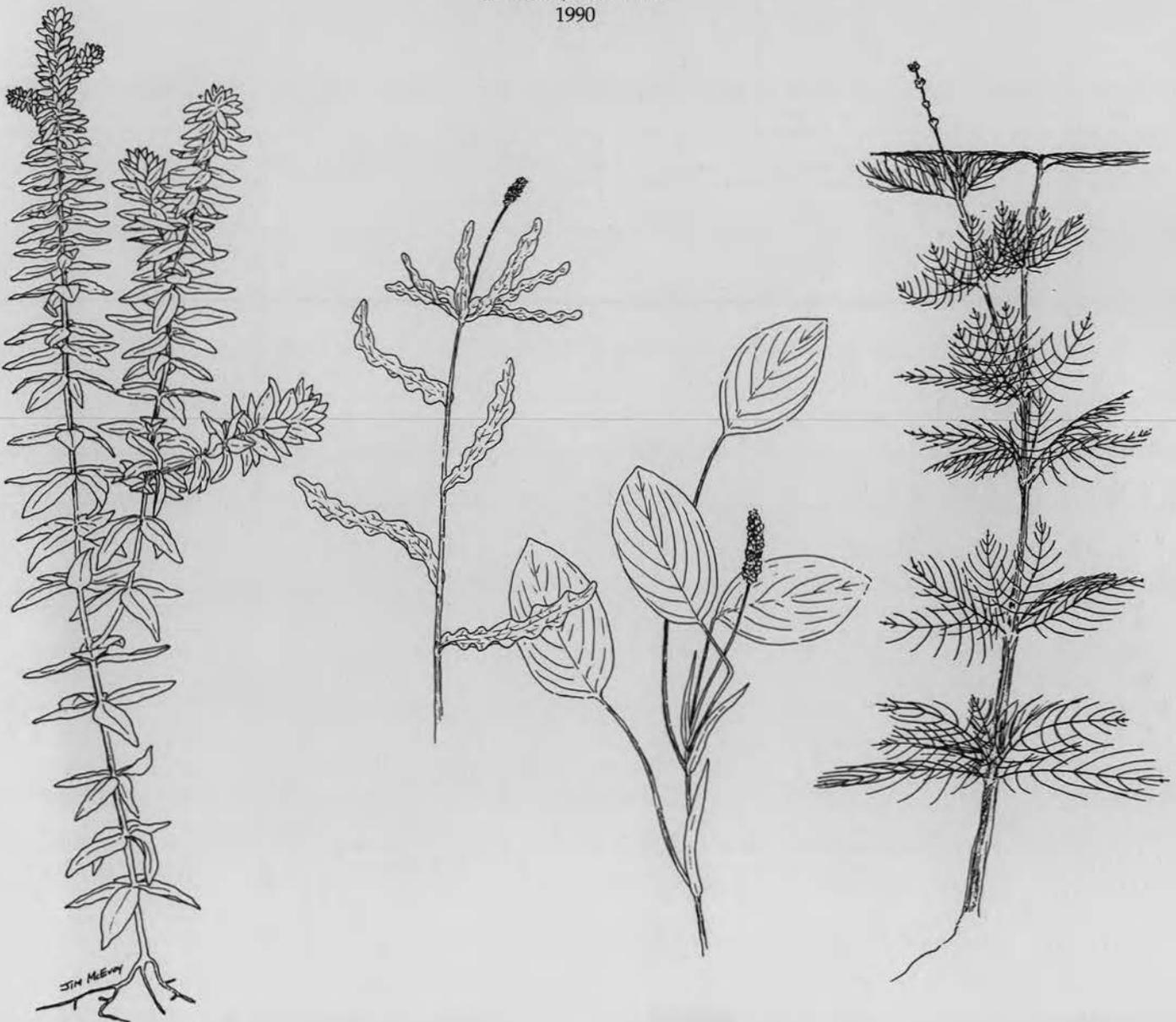

Ecosystem Responses To Growth and Control of Submerged Macrophytes: A Literature Review

Technical Bulletin No. 170
Department of Natural Resources
Madison, Wisconsin
1990



*COVER: Elodea, curly-leaf pondweed, floating-leaf pondweed, and Eurasian water milfoil.
Drawings by Jim McEvoy.*

ABSTRACT

Submerged macrophytes alter the physical, chemical, and biological makeup of aquatic ecosystems. The plants improve water clarity by preventing shore erosion, stabilizing sediment, and storing nutrients needed by algae. They cast shade and retard water movement, creating vertical temperature gradients. Their photosynthesis and respiration cause daily fluctuations in pH, alkalinity, and concentrations of dissolved oxygen and carbon dioxide. Even the lake bottom is altered from oxidation of organic matter in decaying plants. Living foliage provides substrate for invertebrates, shelter for fry, and food for water birds.

Herbicides and harvesting impact ecosystems directly by killing plants and animals and indirectly by destroying habitat. Herbicides leave plants to decay, causing loss of dissolved oxygen and release of nutrients. Harvesting removes plants with their nutrients, but disrupts invertebrate habitat and exposes fry to predation. Both treatments can lead to algal blooms, poor water clarity, and shifts in plant community composition.

Lake managers can reduce unwanted ecosystem change by thoughtful planning and judicious treatment. Integrating several techniques, each used only when and where needed, can improve control and reduce harm to the ecosystem. Rather than being tools of destruction, herbicides and harvesting can build more useful and diverse ecosystems.

KEY WORDS: bluegill, harvesting, herbicides, invertebrates, largemouth bass, macrophytes, phytoplankton, water birds.

ECOSYSTEM RESPONSES TO GROWTH AND CONTROL OF SUBMERGED MACROPHYTES: A LITERATURE REVIEW

By Sandy Engel

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Box 7921, Madison, Wisconsin 53707
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The earth's vegetation is part of a web of life in which there are intimate and essential relations between plants and the earth, between plants and other plants, between plants and animals. Sometimes we have no choice but to disturb these relationships, but we should do so thoughtfully, with full awareness that what we do may have consequences remote in time and place.

Rachel Carson, Silent Spring

PREFACE

The macroscopic flora of lakes form vibrant communities, affecting and affected by the aquatic ecosystem. Some people view the plants with wonder, marveling at their form and function. Most treat them as aquatic nuisances; they denude shorelines to improve recreation or navigation, unaware of how water quality and other biological communities depend on macroscopic plants.

Considerable knowledge is needed to properly manage lake vegetation.

Busy managers find little time for literature searching that would help them consider the full consequences of plant control programs.

Lake managers will find this report both a review of macrophyte ecology and a synthesis of literature on plant growth and control. It takes a panoramic view of macrophyte communities, citing 111 references and emphasizing conditions and species widely found in fertile Midwestern lakes. This approach complements Technical Bulletin No. 156

(Engel 1985), which focuses on a single macrophyte community and its experimental harvesting.

I hope this report will encourage an ecosystem approach to lake management, a respect for all living organisms, and a use of technology that creates rather than destroys.

Sandy Engel
August 1987

INTRODUCTION

Submerged **MACROPHYTES*** dominate the shallows of many lakes during summer. Exposed shallows become underwater meadows—habitats for animals and other plants. Water quality changes as the plants grow and metabolize. Even sediment is altered by plant growth and decay. But macrophytes exert control beyond the shallows.

Disturbing macrophyte communities with chemical herbicides or mechanical

harvesters can cause widespread but subtle **ECOSYSTEM** changes. Predicting such consequences, or choosing an appropriate treatment, requires knowledge of the roles and interactions of macrophyte communities.

This report is a technical guide for lake managers. First, it reviews the physical, chemical, and biological effects of macrophyte communities. Next, it explores how ecosystems resist change and mask treatment responses. Then, it

looks at ecosystem impacts on both nuisance plants and organisms not intended for control. This ecological background leads to a review of herbicide and harvesting impacts. Finally, the report considers how managers can integrate these techniques with others to reduce ecological harm and even improve ecosystems.

* All terms defined in the glossary are shown in **BOLDFACE** type the first time they appear in the text.

MACROPHYTE COMMUNITY DYNAMICS

Shaping the Physical Environment

Blocking Water Movement

Underwater macrophytes alter the physical environment by intercepting water movements and sunlight. Dense vegetation creates quiet pockets near shore and reduces turbulence from breaking waves, longshore currents, and **RUNOFF** (Madsen and Warncke 1983). Plants at the water surface blunt the wind, reducing its potential to rework the shore and stir the bottom. High-energy shores, exposed to erosion from winds and waves, become calm depositional plains after plant growth. Such protected areas attract other macrophytes, including rootless species.

Plant beds trap particles entering lakes in runoff and change underlying sediment. Underwater foliage acts as a screen to collect large soil particles. Reduced turbulence within plant beds permits smaller particles to settle, leaving the finest particles for transport offshore. More sediment is added as plants slough leaves and die. Organic matter in the sediment attracts microorganisms and larger **INVERTEBRATES** that break down the particles. Remaining sediment, shaped by mechanical and biological events, thus accumulates as an aggregate of particles with diverse origins.

Casting Shade

Leaves and stems intercept sunlight. Plants with grasslike leaves permit more sunlight through the water than those more finely dissected (Fig. 1). Floating mats of green algae, such as *Spirogyra*, also block sunlight. A canopy of surface foliage can further reduce sunlight and shade underlying plants. For example, a canopy of water crowfoot (*Ranunculus fluitans*) just 10 cm (4 inches) thick eliminated 99% of light striking an English chalk stream (Westlake 1964).*

Plant canopies reduce light for other species. The shade conceals prey and hinders feeding by fish dependent on sight. Adult largemouth bass (*Micropterus salmoides*), for instance, often cannot see fry among plant stems (Savino and Stein 1982) and grow poorly in lakes with dense macrophytes (Engel 1987a).



Sediment entering Lake Mendota, Wisconsin, is held along shore by beds of submerged macrophytes. (A June 1981 photo of Warner Park, Madison, Wisconsin, by Thomas M. Bainbridge.)

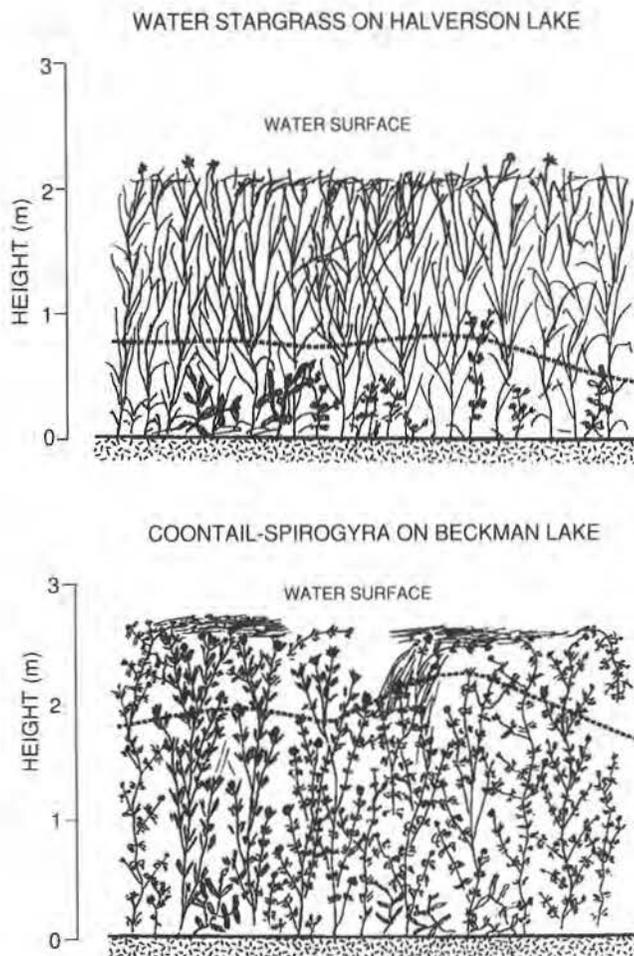


FIGURE 1. Macrophyte beds in Halverson and Beckman lakes, southern Wisconsin, showing depths of 10% light level (dotted lines). Water stargrass, with linear leaves, admits more sunlight than does coontail, with dissected leaves.

** Common and scientific names of aquatic plants mentioned in this report are listed in the Appendix.

Plant species can adapt to poor light. Many pondweeds (*Potamogeton* spp.) grow floating "sun" leaves as well as underwater foliage (Sculthorpe 1967). Eurasian water milfoil (*Myriophyllum spicatum*) sloughs lower leaves that merely respire and concentrates its foliage at the water surface (Titus et al. 1975). Coontail (*Ceratophyllum demersum*) and elodea (*Elodea canadensis*), growing beneath taller plants, concentrate **CHLOROPLASTS** in cells at the periphery of leaves to capture the most light (Best and van der Werf 1986). Such adaptations enable plants to spread when competing foliage is removed.

Retarding Heat Transfer

In casting shade and blocking water movement, plant beds retard heat transfer to the bottom. The foliage acts as a barrier to keep warm water at the surface and cool water at the bottom. This temperature difference can reach 10 C (18 F) on hot summer days (Dale and Gillespie 1977). Density differences between the water masses help maintain the separation. Surface foliage also converts sunlight to heat, warming the water surface to over 30 C (86 F) in sunny areas (Fig. 2).

These temperature gradients create warm and cool **MICROCLIMATES** for colonizing organisms (Engel 1985). Animals unable to withstand warm water can approach the shore under a protective cover; others can be repelled by heat radiated from surface foliage. Cool bottom water can also reduce photosynthesis in lower leaves and delay hatching of fish eggs, whereas warm surface water can speed development of invertebrates. Microclimates thus diversify the inshore zone and add complexity to the ecosystem.

Altering Sediment and Water Chemistry

Using Carbon and Oxygen

Photosynthesis and respiration in dense beds can alter the chemical composition of lake water. Photosynthesis enables green plants to convert carbon dioxide to organic carbon. But **FREE CARBON DIOXIDE** disappears from lake water when pH exceeds 8.46 (Hutchinson 1957). Stoneworts (*Chara* spp.), elodea, Eurasian water milfoil, and some potamogetons can shift to bicarbonate and continue to photosynthesize (Prins et al. 1982). They then can grow in alkaline waters and reach densities that require treatment. Other plants, such as quillworts (*Isoetes*), cannot use bicar-

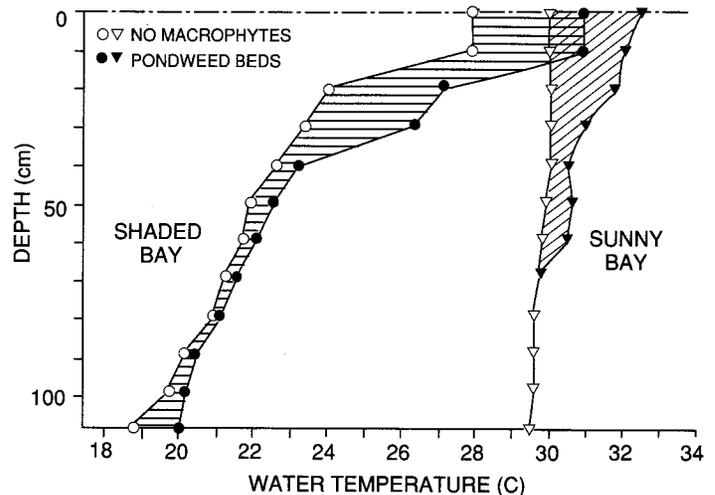
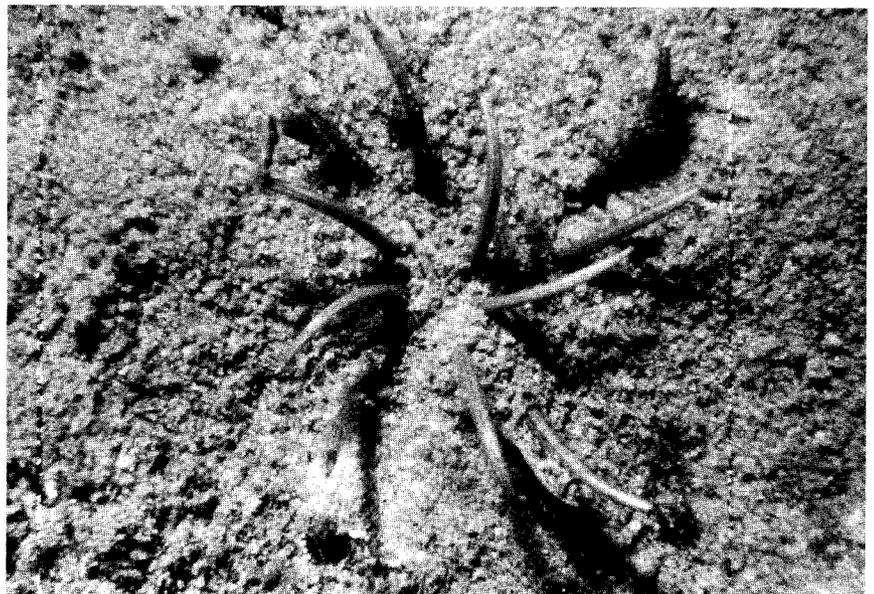


FIGURE 2. Temperature profiles through and outside pondweed beds in shaded and sunny areas of Halverson Lake, Wisconsin (Engel 1985).



Isoetids, like these quillworts (*Isoetes macrospora*), use only carbon dioxide in photosynthesis and thus are restricted to soft water. (Photo in Crystal Lake, Vilas County, Wisconsin, by Douglas W. Stamm.)

bonate and grow mainly in soft waters (Barko et al. 1986). Eurasian water milfoil also stores free carbon dioxide in tissue spaces during respiration at night.

Photosynthesis elevates dissolved oxygen, pH, and **ALKALINITY** during the day; respiration reverses them at night (Kulshreshtha and Gopal 1982). During the day in an elodea bed (280 mg dry weight/m²), for example, dissolved oxygen rose from 6 to 14 mg/L, pH from 7.5 to 9.5, and total alkalinity by 100 mg/L (Ondok et al. 1984). Dissolved oxygen can become depleted at night. Reduced turbulence within dense

plant beds helps produce these levels, creates vertical chemical gradients, and isolates the water column (Hutchinson 1975, Madsen and Warncke 1983).

Such chemical changes affect invertebrates and fish using the plant beds. Photosynthesis removes carbon dioxide from lake water and causes inorganic carbon to precipitate on plants and rocks as **MARL**. These deposits, mostly comprising calcium and magnesium carbonate, interfere with herbicide activity (Gangstad 1986) and keep some insects off the plants. Respiration at night can reduce dissolved oxygen enough to kill

sessile rotifers, clams, and sluggish snails; fish and swift invertebrates can flee to areas that may expose them to predation. Largemouth bass and bluegill (*Lepomis macrochirus*) in aquaria, for example, avoid water with 1.5 mg/L of dissolved oxygen (Warren et al. 1973). Poisonous gases, such as hydrogen sulfide and methane, can collect from microbial decomposition of plant matter. Thus plant metabolism can produce lethal and sublethal conditions that alter the composition of inshore communities.

Building Sediment

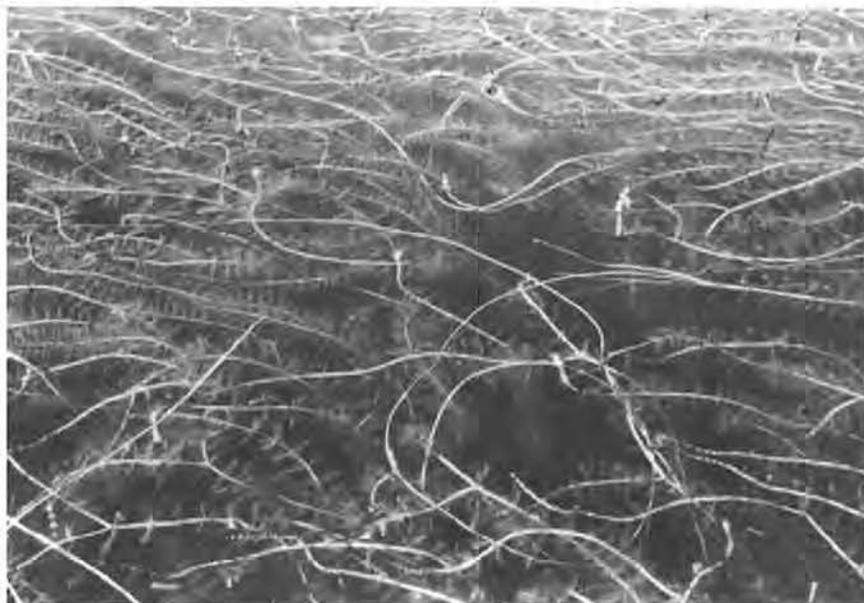
Aquatic macrophytes build and modify lake sediment. Sloughing of leaves and stems contributes organic matter and inorganic nutrients needed for decomposition. Bacteria, fungi, protozoans, and rotifers are principal decomposers, but crayfish and certain insects graze and shred soil particles. Macrophytes thus support a complex array of bottom organisms.

Decomposition is complete when organic matter has converted to carbon dioxide and water. Sediment however contains minerals and organic matter that resist decay. For example, leaves of submerged macrophytes take several weeks to decay in summer, but terrestrial leaves can remain for a year (Pieczyńska 1986). Because decay is rarely complete, organic matter builds sediment and lakes become shallower. The accumulating organic matter can eventually inhibit plant growth (Barko and Smart 1986).

Mining Nutrients

Plants need nitrogen and phosphorus to grow and reproduce. The nutrients are extracted ("mined") as ammonium ions, nitrate ions, and dissolved phosphorus. Although rooted plants can take dissolved phosphorus from lake water (Carignan and Kalff 1980), sediment typically has the greatest supply and thus becomes the principal source of phosphorus (DeMarte and Hartman 1974, Welsh and Denny 1979). For instance, Eurasian water milfoil in Lake Wingra, Wisconsin, took 73% of its tissue phosphorus from sediment (Adams and Prentki 1982). Rooted species differ however in whether they rely on lake water or sediment to obtain nitrogen (Denny 1980, Reddy and DeBusk 1985). Rootless species, such as coontail, extract nutrients from sediment only when they rest on the bottom.

Sediment around roots stays warmer, coarser, and better aerated than sediment in deep water or far below roots (Jones 1985). Roots release dissolved oxygen, aerating the soil. These condi-



Eurasian water milfoil extracts nitrogen and phosphorus from sediment or lake water to produce dense canopied beds. (A September 1986 photo of Devils Lake, Sauk County, Wisconsin, by Richard A. Lillie.)

tions favor breakdown of organic carbon to carbon dioxide and organic nitrogen to nitrate. But phosphorus binds to clay, iron, manganese, or aluminum salts and becomes unavailable to plants.

Microbial decomposition and respiration by roots and animals in sediment, however, deplete dissolved oxygen and liberate dissolved phosphorus (Wium-Andersen and Andersen 1972). Ammonium ions and phosphorus then become available to roots. The sediment blackens from ferrous sulfide deposits or gives off a smell of hydrogen sulfide gas.

Whether sediment beneath macrophytes stays aerated, and to what extent nutrients become available to rooted plants, depend on how much oxygen is released and consumed by chemicals and organisms in the sediment (Carpenter and Lodge 1986).

Storing and Releasing Nutrients

Macrophytes store and release nutrients as though capacitors in an electrical circuit. Nutrients move up to leaves or



The author holds the tuberous rhizome of a water lily, used to store carbohydrates made in leaves. (A 1977 photo of South Twin Lake, Waupaca County, Wisconsin, by Wendell J. Wojner.)

down to roots. Tissue concentrations differ among plant species, among plants of the same species, and within the plants (Engel 1985). Concentrations drop when plants decay in late summer (Richardson 1974). Either phosphorus or nitrogen can limit growth (Gerloff and Krumbholz 1966), but plants can store both nutrients in excess of biological need.

Macrophytes also store heavy metals, including some needed in trace amounts. Aluminum, antimony, arsenic, boron, cadmium, cobalt, copper, iron, lead, mercury, selenium, and zinc have been reported in many macrophyte species (Stanley 1974, Mudroch 1980, Baudo et al. 1981). Some metals are essential parts of plant enzymes and stimulate growth in low concentrations. Higher levels produce yellowing, stunting, deformity, or increased risk of disease. Copper, needed in trace amounts to form enzymes, becomes a herbicide at higher dosage.

Plants release nutrients and heavy metals mainly when shoots decay (Nichols and Keeney 1973, Godshalk and Wetzel 1978). Those lost from basal leaves quickly enter the sediment, but canopy formers, such as Eurasian water milfoil, release nutrients far above the sediment. The nutrients can then spread into the PELAGIC ZONE to stimulate PHYTOPLANKTON (Landers 1982). For instance, water milfoil leaves slough continually, releasing nutrients slowly to the water. But these nutrients at first fuel canopy development rather than phytoplankton blooms. Herbicide treatment or natural die-offs of macrophytes, however, flush nutrients into the water where they can more likely stimulate algal blooms (Morris and Jarman 1981). Using herbicides to shift community composition from bottom-spreading to canopy-forming species can alter nutrient cycling in lakes.

Acting as Sink or Source

Nutrient concentrations in open water depend on whether the macrophyte community acts as a nutrient sink or source. As a sink, the community stores nutrients in foliage and traps particles in runoff. As a source, it releases nutrients from decaying foliage and fails to impede runoff. Nutrients then increase in the pelagic zone and can stimulate phytoplankton.

By decaying mainly at the end of their growing season, many pondweeds act first as a nutrient sink and later as a source. Eurasian water milfoil, in contrast, can fail to intercept spring runoff when it sheds its lower leaves (Adams and Prentki 1982). Algal blooms then

occur earlier than in lakes with macrophytes in full leaf until fall. Macrophyte control can likewise expose lake water to runoff, permitting nutrients to increase in open water and stimulate algal blooms.

Macrophytes as Habitat

Making Room for Invertebrates

Submerged macrophytes provide food, shelter, and substrate for a variety of organisms. Bacteria, algae, protozoans, rotifers, and larger invertebrates

colonize underwater leaves and stems. Some live on roots. Rotifers and small crustaceans filter bacteria and algae from water flowing by the plants. Snails, certain leeches, and many insect larvae scrape algae and DETRITUS that coat the foliage or settle beneath it. They in turn are consumed by other aquatic insects, as part of a FOOD WEB leading to fish, water birds, and some furbearers.

Macrophytes expand the substrate available to organisms. Plants have 30-50 times as much area as lake bottoms (Edwards and Owens 1965). The dissected leaves of water milfoil and coontail (Fig. 3) provide more area than the ribbon-like leaves of water stargrass

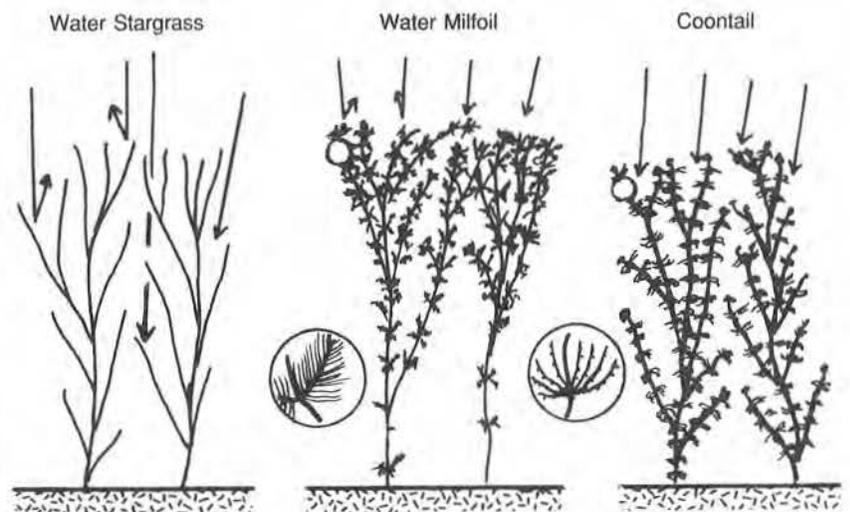
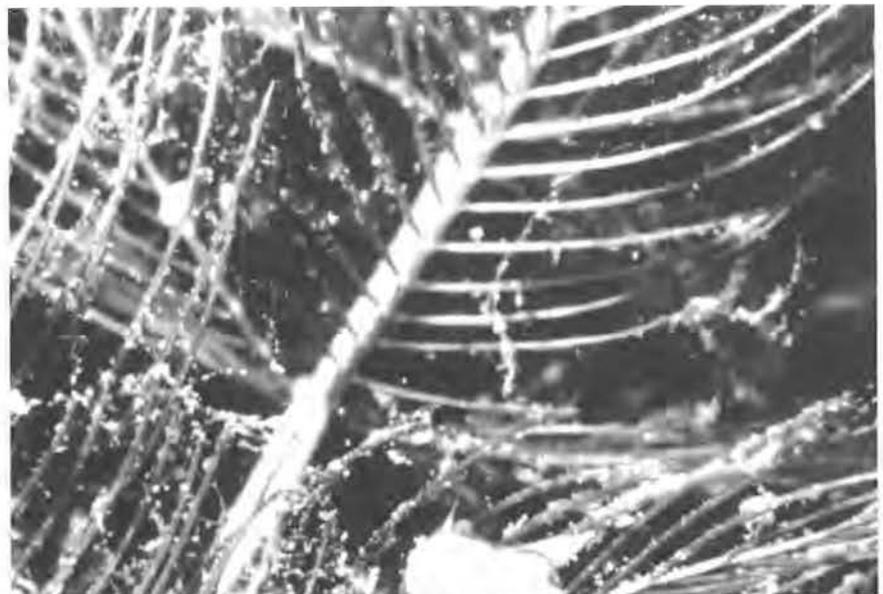


FIGURE 3. Profiles of three underwater macrophytes, showing how their shoots intercept or admit sunlight. Single leaves are enlarged to show arrangement of leaflets.



Leaves of Eurasian water milfoil are split into thread-like leaflets, expanding the surface area for invertebrates to colonize. (Photo of Devils Lake, Sauk County, Wisconsin, by David W. Marshall.)

(*Heteranthera dubia*) and wild celery (*Vallisneria americana*). They thus support more invertebrates (Krecker 1939, Mrachek 1966). Narrow-leaved pondweeds also have large leaf surfaces and are more desirable because they seldom clog waterways or interfere with boating.

Variogated plant beds diversify substrate for invertebrates to colonize. In an Ontario lake, for instance, mixed stands of pondweeds and wild celery supported 3-8 times as many large invertebrates and fish as did pure stands of Eurasian water milfoil (Keast 1984). Such plant beds provide **MICROHABITATS**, such as stems to pierce and leaves to chew. Some invertebrates seem to prefer certain plants, perhaps because of algae coating the shoots (Miller et al. 1989). Plant diversity thus helps segregate invertebrate species and expand feeding opportunities. Seasonal die-offs of plant populations are less likely to disrupt invertebrate communities when some plants continue to flourish.

Invertebrates congregate beneath macrophytes as well. Some use plant remains as food and shelter. Others browse algae coating the sediments. Large invertebrates in a Wisconsin impoundment, for example, were significantly ($P < 0.05$) more numerous and diverse beneath macrophytes than on offshore sediment (Fig. 4). The inshore sediment contained about 60% of all midge larvae (Diptera: Chironomidae) and over 90% each of snails (Gastropoda), fingernail clams (Bivalvia: Sphaeriidae), and larvae of caddisflies (Trichoptera), damselflies and dragonflies (Odonata), and mayflies (Ephemeroptera) during summer (Engel 1985, 1988a). Invertebrates ultimately benefit when macrophytes both grow and decay.

Screening Fish Movements

Submerged macrophytes selectively restrict fish movements. For instance, small bluegills can move freely among the interlacing leaves and stems or can hide from predators (Werner et al. 1981). Bluegill predators, such as largemouth bass, hunt poorly in dense foliage (Savino and Stein 1982, Engel 1985). Their growth declines after only 2 or 3 summers of life in densely planted waters (Fig. 5).

Bluegill can become crowded in dense macrophyte beds, causing overpredation and eventual stunting. Sparse vegetation however exposes small fish to predation. Bluegill growth and bass production appear greatest at intermediate densities of underwater macrophytes (Crowder and Cooper

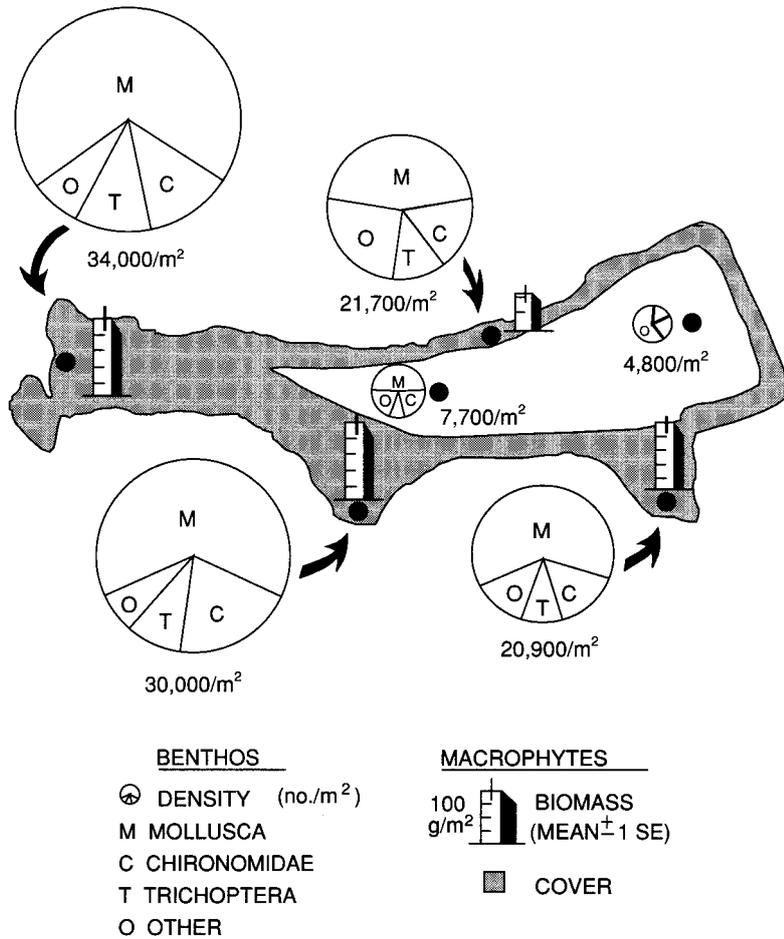


FIGURE 4. Macrophyte cover and mean summer density of large, bottom-dwelling invertebrates (BENTHOS) dredged at 6 sites in Halverson Lake (Engel 1988a).

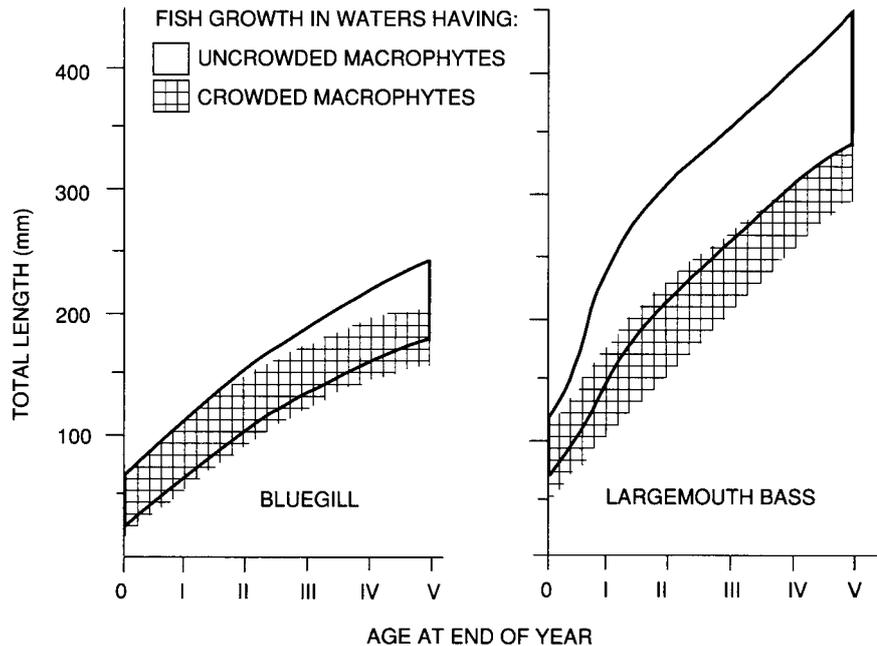


FIGURE 5. Growth of bluegill and largemouth bass in 300 Midwestern waters with crowded or uncrowded macrophytes.

1982, Wiley et al. 1984). A loose arrangement of broad- and narrow-leaved plants provides enough cover for fry and enough fry for predators. Selectively channeling dense macrophyte beds by mechanical harvesting can create cruising lanes for predators (Engel 1987a).

Enriching Plankton Communities

Macrophytes enrich PLANKTON communities. Some algae and invertebrates, preferring to live on or near plant beds, become swept into open water where they reproduce. For instance, many kinds of diatoms, green algae, rotifers, and small crustaceans occur principally inshore, but frequent the plankton of open water. Such pond plankton (Hutchinson 1967) diversify energy pathways leading to fish and waterfowl production. Controlling macrophytes would enlarge the open water zone, but indirectly reduce its species richness.

Supporting Waterfowl

Waterfowl need submerged macrophytes as food. They consume seeds, tubers, foliage, and plant-dwelling invertebrates (Jahn and Hunt 1964). Even fish-eating common loons (*Gavia immer*) browse macrophytes (Palmer 1962). *Chara* (*Chara* spp.), naiads (*Najas* spp.), wild celery, horned pondweed (*Zannichellia palustris*), and many potamogetons are favorite waterfowl foods (Nichols 1986). Some plants, such as coontail and elodea, are more valuable for the invertebrates they harbor; others, like broad-leaved pondweeds and wild celery, have edible parts but few invertebrates. A diverse macrophyte community offers the best feeding for a variety of waterfowl.

Many waterfowl change diet. Breeding hens often switch from eating foliage to invertebrates before laying. Ducklings also eat invertebrates but shift to seeds, tubers, or shoots as they develop (McAtee 1939, Low and Bellrose 1944). Adult canvasback ducks (*Aythya valisineria*) eat invertebrates in summer, then select tubers of wild celery and sago pondweed in fall. Common goldeneye (*Bucephala clangula*) and lesser scaup (*A. affinis*) add vegetation to their invertebrate diets in winter (Jones and Drobney 1986). Controlling macrophytes thus could eliminate foods critical to certain waterfowl.

Like fry and spawning fish, ducklings and laying hens need a diet rich in protein and carbohydrate. Macroinvertebrates, seeds, and tubers represent food concentrates. Macroscopic in-



An elodea bed in Devils Lake, Sauk County, Wisconsin, sheltering bluegill and providing habitat for their invertebrate prey. (Photo by David W. Marshall.)



Canvasback ducks dive for invertebrates and buried tubers of sago pondweed (*P. pectinatus*) and wild celery—high-energy foods needed for breeding, growing, and migrating. (Photo on Delta Marsh, Manitoba, by Gerald A. Bartelt.)

vertebrates when dried contain 40-70% protein and average 5 kcal/g (Driver 1981). Seeds and tubers contain over 10% protein by weight and about 4 kcal/g (Donnermeyer and Smart 1985), whereas submerged leaves have less than 2% protein and more than 10 times the water content (Moyle 1961).

Waterfowl decline seems related to habitat degradation in several Wisconsin lakes, including Lakes Butte des Morts, Koshkonong, Winnebago, and Winneconne (Jahn and Hunt 1964). The Madison lakes were fall staging grounds for diving ducks (*Aythya* spp.) until pondweeds and wild celery were replaced by Eurasian water milfoil in the 1960s (Vander Zouwen 1983). Expansion of wild celery beds on pools of the

Upper Mississippi River, in contrast, has attracted fall migrating canvasbacks (Serie et al. 1983, Korschgen and Green 1988). These examples show the importance of plant habitat to waterfowl, but human disturbances and other factors are also important.

ECOSYSTEM RESPONSES

How Ecosystems Change

Negative Feedbacks

Natural ecosystems are complex associations of microbes, plants, and animals linked by food transfer. Food chains, leading from herbivores to carnivores and decomposers to grazers, interlock as food webs. These alliances act as **NEGATIVE FEEDBACK LOOPS** to help ecosystems dampen outside disturbances (Margalef 1968).

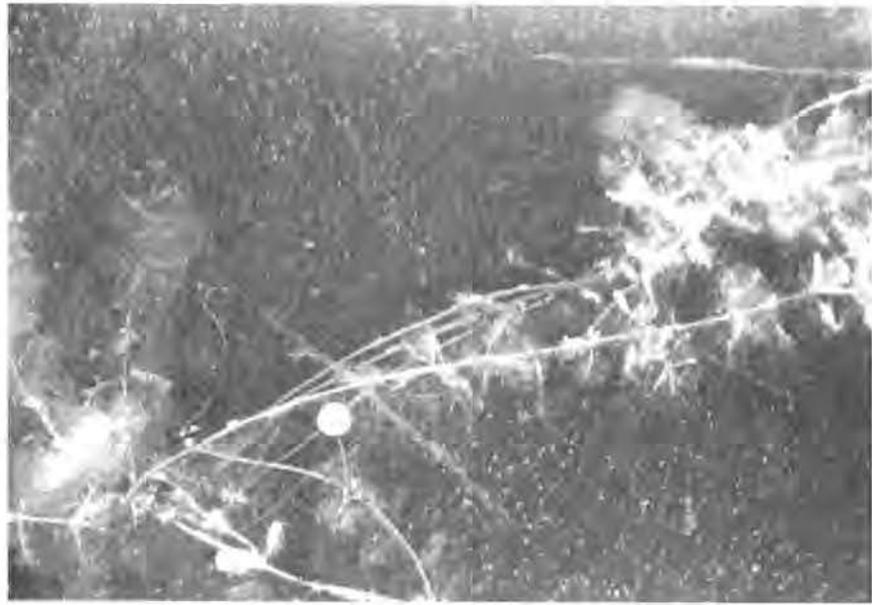
Think of home heating, and you have a negative feedback loop. Cold drafts cause a thermostat to trip a furnace, blasting heat through the house and restoring inside temperature. Add central air conditioning, and the same thermostat controls temperature year-round. Now the "blaze of noon" or "the bite of winter" hardly disturbs the home system.

Lake ecosystems have negative feedback loops as well. Suppose spring rains wash fertilizers into a lake, turning the water green with algae or macrophytes. Water fleas that graze algae respond by feeding and multiplying. Eventually the tiny herbivores keep the algae in check. Fish in turn keep the water fleas in check, or the water fleas decline with their prey. This simple food web acts like a thermostat: increase in prey (rise in summer heat) is counteracted by increased predation (air conditioner tripped by thermostat). Macrophyte growth stops too when nutrients run low. Other negative feedbacks work in lakes, as they do in homes, to resist change and thus stabilize the system.

In partitioning food and space, a varied macrophyte community maintains the negative feedbacks needed for ecosystem stability. Habitat for invertebrates gives predators a choice of prey. Such diverse ecosystems have long food chains, with many **TROPHIC LEVELS**. Energy and materials transfer in many directions, whereas disturbances remain localized. Loss of one kind of invertebrate, for instance, may cause a predator merely to shift diet. Macrophytes, therefore, help ecosystems resist disturbances.

Positive Feedbacks

But feedback loops can be overwhelmed. Continual loss of prey (like overheating a room) can starve predators with little else to eat. Through de-



Shoots of Eurasian water milfoil freeze into lake ice and then decay after ice out; new shoots grow from wintering root crowns beneath old shoots. (Photo of Devils Lake, Sauk County, Wisconsin, by Sandy Engel.)

cay and filtering runoff, macrophytes add nutrients to sediment and thus stimulate more growth. Such **POSITIVE FEEDBACK LOOPS** are vicious cycles that alter the composition of ecosystems and the transfer of energy and materials.

Macrophyte control destroys microhabitats, shortens food chains, and opens the lake bed to invasions by exotic plants. Predators have few prey choices. The ecosystem may not recover quickly. Formerly diverse plant beds become monotypic stands even more crowded than before control. How fast the sites regrow depends on which plants colonize and dominate.

Plant Invasions

Submerged macrophytes colonize disturbed sites using seeds, axillary buds formed on shoots, tubers formed on **RHIZOMES**, and leaf fragments (Sculthorpe 1967). Water birds carry seeds in their feathers, feet, and stool. People unwittingly carry plant **PROPAGULES** and foliage on boats, trailers, and motor shafts and propellers. The propagules survive in lake sediment and develop when conditions improve. Removing canopy foliage, for example, can increase sunlight and water temperature enough to stimulate development.

Invasions of Eurasian water milfoil in North America and elodea in Europe

illustrate how exotic species can dominate native flora (Sculthorpe 1967, Nichols and Shaw 1986). These species winter under lake ice as green shoots. When ice melts in late winter and the water warms, buds form quickly on old shoots (elodea) or wintering root crowns (water milfoil). Elodea soon carpets the bottom, whereas water milfoil covers the water surface. Both species block sunlight and crowd competitors that develop more slowly from propagules on the bottom. Controlling native species can even encourage these exotics. Dominance by water milfoil or elodea means a longer growing season, because they sprout earlier and keep their leaves longer than many native species. Plant habitat remains longer for invertebrates, nutrients stay trapped in the **LITTORAL ZONE**, algal blooms are delayed, and gamefish remain separated from inshore prey (Engel 1985).

Many ecosystem changes go unnoticed. Ecosystems are so complex that detailed studies, begun before the changes, are needed. Even obvious replacements, such as wild celery by water milfoil, can escape notice or have happened so long ago that no one remembers. Untrained observers fail to recognize changes in bottom fauna or plankton. Some changes are missed because they happen when few people visit the lake. Lake studies begun too late can also miss the ecosystem changes.

Response Times

Ecosystems respond quickly or with hesitation to such disturbances as macrophyte control. Neighboring lakes can respond differently to the same kind of treatment. Even adjoining basins of the same lake show individual responses. Although they appear similar, ecosystems in these lakes or basins are not structured alike, nor are treatments ever identical. Lake studies can assess how ecosystems respond to treatment.

Immediate responses, occurring within hours of disturbance, are often obvious and temporary. Sediment or runoff can cloud the water just after mechanical harvesting. Some herbicides, like copper sulfate, can discolor lake water for a few hours. Mechanical harvesters release some plant fragments to drift onto downwind shores. Dead fish and invertebrates can appear after treatment but could be natural mortalities or due to angling. Although temporary, such responses can signal more fundamental changes to come.

Short-term responses occur within days or weeks of disturbance. They include loss of plant habitat, yellowing of surviving plants, odors from decomposing plants and animals, and regrowth of algae or macrophytes. Plant-dwelling invertebrates can decline from habitat loss, but bottom dwellers can increase (Hilsenhoff 1966). Loss of shelter can expose young fish to increased predation. Loss of macrophyte cover can increase bank erosion and suspension of bottom sediment, especially from motorboat activity. Water birds can disperse to quiet waters with protective cover and food. Oxygen depletion from plant decomposition can cause local fish kills. Algal blooms can follow herbicide treatment, as decomposing macrophytes release nutrients (Landers 1982).

Delayed responses are subtle, taking months or years to develop. Ecological succession can occur, as pioneer plants like chara invade disturbed areas and then are replaced by rooted species (Engel and Nichols 1984). Treatment-tolerant species can dominate after repeated control of other species. For example, yearly harvests of canopy foliage can increase sunlight penetration and eventually stimulate growth of underlying wild celery (Engel 1990). Prolonged herbicide use can cause enough nutrient release from decaying macrophytes to accelerate eutrophication, causing increased phytoplankton and loss of submerged macrophytes (Phillips et al. 1978). Plant and animal species can disappear after treatment, surviving in lake sediment as seeds, spores, or cysts. Seeds



Blue-green algae streaked the water surface of this pond when macrophytes died and released nutrients. (A September 1987 photo of Halverson Lake, Iowa County, Wisconsin, by Sandy Engel.)



Growing beneath floating scums of algae, wild celery thrives despite yearly mechanical harvesting. (A July 1989 photo of Montello Lake, Marquette County, Wisconsin, by Richard B. Kahl.)

of many macrophyte species even germinate better after lying dormant at 1-3 C (34-37 F) (Muenscher 1936). They can develop months or years later.

The Nature of Impacts

Macrophyte control has ecological, social, and economic impacts that result directly or indirectly from treatment.

Direct impacts affect organisms sensitive to treatment. Although nuisance plants are targeted for control, many

species of plants and animals can be just as sensitive and become unintended victims of control. For example, crustaceans like *Daphnia* and amphipods are sensitive to many herbicides used to treat algae or macrophytes and disappear upon treatment (Gangstad 1986). Algae can be just as sensitive as macrophytes to certain herbicides, but usually are quicker to recover.

Indirect impacts of plant control affect organisms tolerant of treatment but dependent on sensitive species. Plant-dwelling algae and invertebrates lose

habitat when macrophytes are controlled. Even bottom dwellers are affected, as waves dislodge rootless plants or heat-sensitive invertebrates cannot find a cool microclimate in the denuded shallows.

Fish and waterbirds also lose food and habitat when macrophytes are controlled. Young fish seeking shelter in plant beds become exposed to predation by other fish. Large **ZOOPLANKTON** can disappear, as young fish shift from preying on plant-dwelling invertebrates to eating zooplankton. Algal blooms can then increase as the zooplankton that controlled them decrease. Such **TROPHIC CASCADES** (Carpenter et al. 1985) occur from changes in **BIOMASS** or production of dominant predators.

Indirect impacts also occur from changes in the physical environment and water or sediment chemistry. Water temperature and sunlight increase as surface foliage is removed. Lake water becomes turbid as macrophytes are no longer present to intercept runoff and prevent sediment suspension. Runoff enters the pelagic zone to stimulate phytoplankton, further lowering water clarity (Landers 1982). Oxygen depletion and buildup of toxic gases, such as hydrogen sulfide, result from plant decomposition and can kill invertebrates or drive away fry.

By influencing the usefulness of a water body, macrophyte control has



Floating mats of macroscopic algae mar the beauty of clear lakes and interfere with sailing and other water sports. (A May 1981 photo of Devils Lake, Sauk County, Wisconsin, by Richard A. Lillie.)

social and economic impacts. Plant control opens areas for boating, fishing, and swimming. But these uses are curtailed if plant control lowers water clarity or permits long-season plants, such as water milfoil, to become established.

Lake appearance owes much to the beauty of the shore (Threinen 1964). Although difficult to document, such aesthetic changes affect property values around lakes and the local businesses

that depend on tourism. Fish kills, algal blooms, and beached plants may drive away lake users and discourage real estate buyers. Yet, conflicts arise when some people prefer "solitude and beauty" (Klessig 1985) to motorboating. Such values and potential conflicts must be considered when designing plant control strategies (Engel 1987b, 1989; Nichols et al. 1988).

MACROPHYTE CONTROL

Chemical herbicides and mechanical harvesters are widely used to control macrophytes. Contact chemicals kill plants at the point of treatment, such as leaves or shoots. Systemic chemicals kill plants after moving internally, such as from leaves to roots. Both herbicides leave plants to decay. Harvesters cut and remove vegetation but, like contact herbicides, leave roots and rhizomes unharmed. Herbicides can be applied rapidly from a boat and require less labor and machinery than harvesting. But some herbicides impose a waiting period before drinking or eating fish from the treated water; harvesting immediately frees areas for use. Herbicides also drift into unwanted areas, whereas harvesters can limit the depth and area treated.

Herbicides differ so much in chemical formulation and application that

their various uses constitute distinct management techniques. Different herbicides and their health effects are described by Gangstad (1986). Harvesters, in contrast, function alike and differ mainly in size and engineering details (Cooke et al. 1986).

Herbicide Impacts

Herbicides are toxic to both plants and animals. Species differ however in sensitivity to particular herbicides. Amphipods (*Hyalella azteca*), for example, are more than 500 times as sensitive to diquat (dibromide 6,7-dihydrodipyrido pyrazinedium) as are rainbow trout (*Oncorhynchus mykiss*) (Brooker and Edwards 1975). But amphipods respond more quickly than the trout because survivors can grow and multiply rapidly.

Toxicity

Toxicity varies greatly among herbicides and depends on chemical formula, application, dosage, exposure time, water hardness and pH, flow and flushing rates, and presence of interferences in the water (Gangstad 1986). Toxicity is measured in **BIOASSAYS**, which the U.S. Environmental Protection Agency (EPA) requires to register and classify each herbicide. Tests usually last 24, 48, 72, or 96 hours and measure herbicide concentrations at which 50% of animals die. For example, the herbicide 2,4-D (2,4-dichlorophenoxyacetic acid) is lethal to *Daphnia* but not bluegill fry at a concentration of 3.0 mg/L. Ecological effects of herbicides are not usually given as much attention before EPA approval. Yet, loss of *Daphnia* as prey could starve fry surviving acute herbicide exposure. Only active ingredients are tested, leav-

ing inert ones like surfactants untested. EPA approval of herbicides for general use thus does not mean the chemicals are harmless.

Because toxicity is related to concentration, ecological effects of herbicides vary with dosage. Herbicide concentration in lake water changes soon after application. Drift, **ADSORPTION** onto suspended clay or marl, chemical change, and uptake by plants and animals create "hot spots"—areas where herbicides collect. A "safe" dosage, based on treatment area, cannot exclude ecological harm (Hurlbert 1975).

Herbicides disappear from lake water within a few days or weeks, but some can persist longer in sediment. Diquat adsorbs onto soil particles and can stay in sediment for over 2 years (Berry et al. 1975). Copper sulfate treatments lead to copper contamination of sediment that can affect future plans to deepen a basin by dredging.

Effects of Treatment

Herbicide treatment has lethal and sublethal effects (Fig. 6). Both target and unintended plant species can be killed by the same herbicide, exposed to herbivores, or scattered by water movements. Increased decomposition of dead plants and animals deplete dissolved oxygen in sediment and release nutrients to stimulate plant growth. Loss of canopy foliage can increase sunlight penetration and water temperature, encouraging growth of understory foliage, rootstocks, and vegetative propagules in sediment.

Oxygen loss after treatment occurs from rapid plant decay, resulting at times in fish and invertebrate kills (Brooker and Edwards 1975). Treated macrophytes not only release phosphorus upon decay, but also create **REDUCING CONDITIONS** in sediment for further release of nutrients (Godshalk and Wetzel 1978). Both total phosphorus and ammonium nitrogen increased in an Oklahoma reservoir after water milfoil treatment with 2,4-D (Morris and Jarman 1981). Free carbon dioxide, hydrogen sulfide, and certain heavy metals can be released from sediment when oxygen is depleted.

Broad-spectrum herbicides suppress competitor species, leaving resistant ones to dominate. Diquat, for example, is more effective against native pondweeds than Eurasian water milfoil (Nichols 1986). The latter is sensitive to 2,4-D, but can recover from surviving plants and propagules in sediment. Chara however is resistant to most herbicides, permitting it to rebound after treatment (Hurlbert 1975, Newbold 1976). For instance, it dominated a 1-ha



Spraying herbicides over lake foliage is effective, but the spray can drift and damage valued habitat. (A 1986 photo of a private contractor spraying Blass Lake, Sauk County, Wisconsin, by Carl R. Molter.)

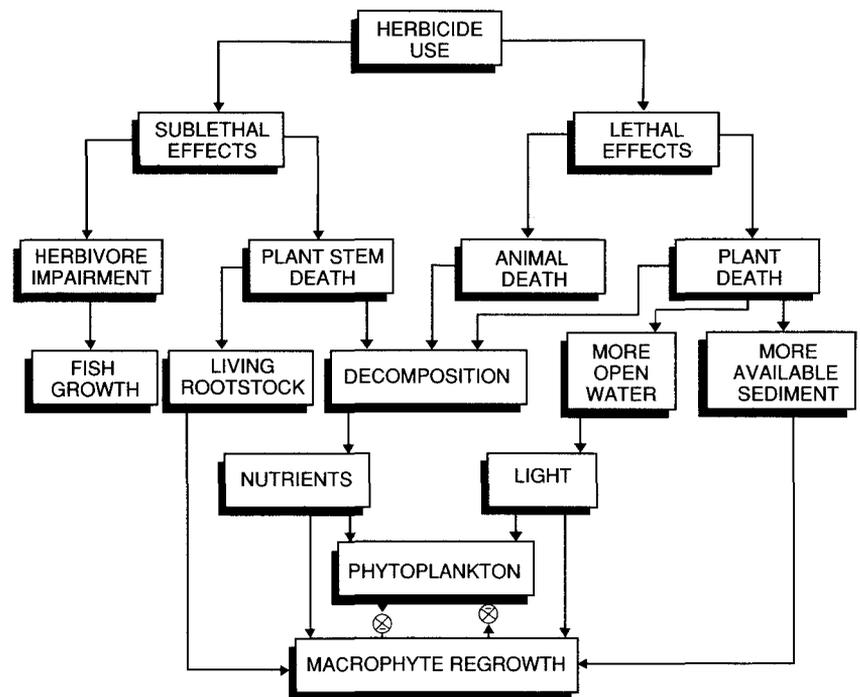


FIGURE 6. A model outlining lethal and sublethal effects of herbicide treatment (simplified from Miller and Trout 1985). Most arrows show increasing responses (more plant deaths cause more decomposition), but two arrows show decreasing responses (more phytoplankton cause less macrophyte growth).

(2.5-acre) plot in Cayuga Lake, New York, after Eurasian water milfoil was eliminated with 2,4-D (Miller and Trout 1985). Marl deposits on plants protect chara from treatment, and plants can invade from untreated areas. Copper sulfate can prevent the algae from dominating, after controlling the rooted plants.

Herbicides intended to kill a variety of plants can ultimately foster plant growth. Rooted plants grew luxuriantly during copper sulfate treatments in the Madison lakes during the 1920s and 1930s, because reduced phytoplankton improved water clarity for macrophyte growth (Domogalla 1935). On the other hand, 2,4-D treatment of Eurasian water

milfoil in North Carolina stimulated a blue-green algal bloom (Getsinger et al. 1982).

Before plants can regrow, herbicides remove habitat for invertebrates. This reduces plant-dwelling invertebrates but can stimulate production of bottom dwellers (Smith and Isom 1967). Bottom organisms increase because more sediment is exposed as habitat, decaying plants add organic matter needed as food, and fish or waterbird predators move away. Fish however can switch to bottom feeding upon loss of plant-dwelling prey. Also, water movements can scour exposed sediment and disturb burrowing species.

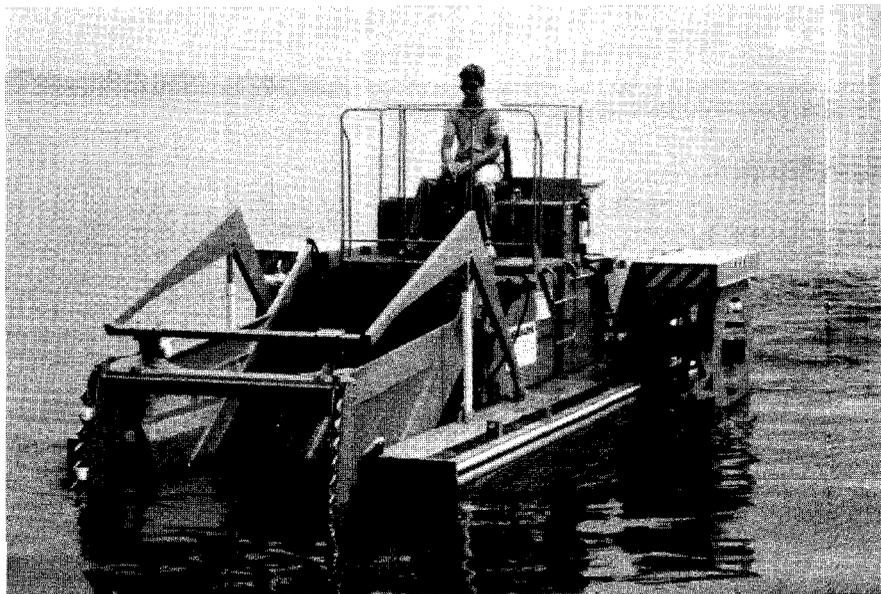
Harvesting Impacts

Immediate impacts occur from cutting plants, disturbing sediment, and removing vegetation. Mechanical harvesters leave plant fragments to create turbidity and drift ashore. Their wake and cutter bars disturb sediment in shallow water, adding to water turbidity.

Effects on Plant Communities

Mechanical harvesting, like herbicide use, alters plant community composition. It removes competitors and opens the lake bed to new growth. Removing shade cast by pondweeds in Halverson Lake, Wisconsin, enabled water stargrass to rise to the water surface and dominate (Engel 1990). Curly-leaf pondweed (*P. Crispus*), growing from resting buds (turions) and rhizomes, can dominate annuals that rely on seeds (Agami and Waisel 1986). Macroscopic algae, spreading from spores and filaments, can colonize as pioneer plants and establish a new succession of plant species (Nichols 1973, Engel and Nichols 1984). Harvesting and herbicides can act together to change plant composition (Nicholson 1981).

Macrophytes often recover quickly from harvesting. Eurasian water milfoil in Ohio and New York lakes, for example, took only a month to fully regrow (Anderson 1984, Mikol 1984). Fragments scattered during harvesting can establish new beds. Cut stems can first divide to produce denser stands (Kimbel 1980). Remaining shoots and roots retain phosphorus and nonstructural carbohydrates, enabling leaves to approach the water surface and photosynthesize (Wile et al. 1979, Perkins and Sytsma 1987). Decades of mechanical harvesting in Wisconsin, often combined with herbicide use, attest to the hardiness of plants like water milfoil.



Mechanical harvesters need water deep enough to operate the rear paddle wheels that drive the machine and its load of plants. (A June 1987 photo of Lake Monona, Dane County, Wisconsin, by Thomas M. Bainbridge.)

Sometimes regrowth is slow, particularly after August harvests (Kimbel and Carpenter 1981) and those harvests separated only by a few weeks (Nichols and Cottam 1972). Slow recovery is possible for coontail because, without roots, it can be completely harvested. (Drifting fragments however can ensure rapid recovery.) Eurasian water milfoil took more than a year to fully regrow from hand pulling or manual cutting in Lake Mendota (Mossier 1968, Nichols and Cottam 1972). Delayed growth could have resulted from removing the shoot tips (apical meristems) or damaging the root crowns.

Some harvester operators claim that harvesting the same area for several years reduces plant growth and thus the number of harvests needed each year (Grinwald 1968). Harvesting does remove propagules and nutrients, and it can shift community composition to slowly growing species. Yet changes in water clarity, weather, and nutrient runoff—conditions independent of harvesting—account for such reductions as well. Eurasian water milfoil declined not only in lakes Mendota and Monona after a decade of harvesting, but also in nearby Lake Wingra, largely unharvested (Carpenter 1980).

Could continual harvesting reduce lake fertility by removing plant nutrients and sediment-forming biomass? Removing all Eurasian water milfoil during its peak in the early- to mid-1970s could have reduced net annual loading of phosphorus by 37% to Lake Wingra (Carpenter and Adams 1978) and 92%

to Ontario's Lake Chemung (Wile 1978). Dissolved organic carbon released by growing or decaying macrophytes (Wetzel and Manny 1972) could have been reduced as well.

If harvesting removed enough nutrients with the foliage, it could delay summer algal blooms or decrease their intensity. Removing 50-70% of coontail and pondweeds in Halverson Lake, Wisconsin, had little effect on phytoplankton until water stargrass invaded harvested areas. Then blue-green algal blooms did not grow (Fig. 7). Yet 5 years later water stargrass declined and dense algal blooms returned (Engel 1988a, 1990).

Such intensive harvesting is rare. It usually removes less than 3% of phosphorus entering lakes each year (Peterson et al. 1974). Even harvesting rough fish in Lake Sallie, Minnesota, took 4-10 times as much phosphorus as did plant harvesting (Neel et al. 1973). Fertile waters typically receive enough nutrients by land runoff to replace those lost to harvesting. More nutrients come from lake sediment during overturn, which can occur throughout summer in shallow bays and lakes. Only where nutrient loading from both the watershed and sediment is insignificant can repeated harvests be expected to retard plant growth (Burton et al. 1979).

Effects on Other Communities

Harvesting removes fish and invertebrates tangled in vegetation (Wile 1978). Many species can be removed, but young-of-the-year sunfish and bass

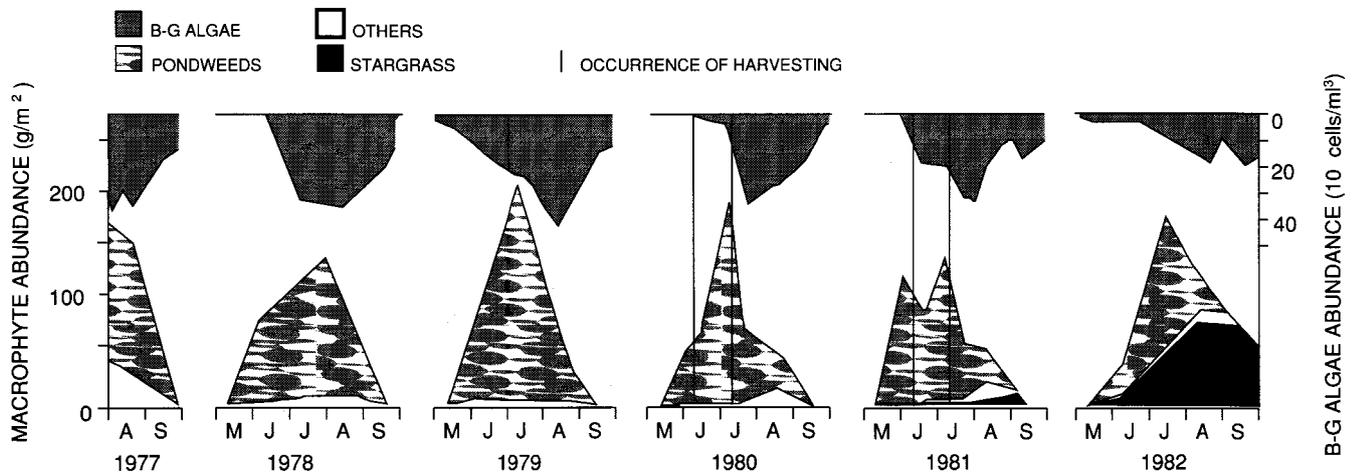


FIGURE 7. Growth of submerged macrophytes and blue-green (B-G) algae in Halverson Lake, before and after plant harvesting. Other macrophytes include mainly coontail and elodea. Harvesting occurred at the paired lines in 1980 and 1981 (Engel 1988a).

are frequent targets (Mikol 1985, Engel 1990). Harvesting can remove as few as 2-3% (Mikol 1984) or more than 30% (Haller et al. 1980) of fish populations in lakes. Avoiding fish spawning and nursery areas, slowing harvester speed, raising the front cutting bar, and leaving escape routes can reduce fish losses.

Many snails and aquatic insect larvae are removed with the plants (Engel 1990). Studies in southern Wisconsin during 1978 found an average of 34 organisms/g dry weight of plants removed during harvesting in Lake Monona (R. Mignery, Wis. Dep. Nat. Resour., unpubl. data) and 13 organisms/g in Okauchee Lake (M. J. Hanson, Wis. Dep. Nat. Resour., unpubl. data). Amphipods, oligochaetes, and larvae of midges (Chironomidae), caddisflies, and damselflies were mostly removed from these lakes. Snails and aquatic insects piled onto shore after harvesting in another lake (Engel 1990).

Harvester machines are so noisy they frighten water birds. For instance, common loons sometimes abandon nesting and brooding when bothered by people motorboating (Zimmer 1979, Titus and VanDruff 1981). Sora rails (*Porzana carolina*) fled a Minnesota marsh when traditional harvesting of wild rice (*Zizania aquatica*) began (Fannucchi et al. 1986). The rails found food and cover on adjacent marshes and stayed away from the original marsh even when harvesting was abandoned.



A handful of bluegill fingerlings picked from a harvester load on Lake Monona, Dane County, Wisconsin. (A 1987 photo of Edwin O. Boebel's hand by Thomas M. Bainbridge.)

Delayed impacts occur when habitat loss alters predation. A **BIOENERGETICS MODEL** for Lake Wingra suggests how removing plant cover could expose young fish to increased predation by older fish (Breck and Kitchell 1979). More zooplankton of larger size would then survive to crop phytoplankton (Bartell and Breck 1979). Algal

blooms however have been observed to increase after harvesting (Neel et al. 1973). They have been stimulated by nutrients from land runoff, bank erosion, exposed sediment, or decay of plant fragments left from harvesting. Whether algal blooms develop after harvesting depends on changes in nutrient dynamics and predation pathways.

ECOLOGICAL CONSIDERATIONS FOR MANAGERS

Herbicides and harvesting must be used wisely. Each has advantages and disadvantages that limit or expand applications. Herbicides work best inshore; harvesting, offshore. Both are useful in clearing areas for boating but can be incompatible with fishing or encouraging desirable plants to grow. Herbicides can be used where harvesters cannot reach, but harvesters are better at clearing boat channels and protecting adjacent habitat. Which method to choose thus depends on the makeup of the ecosystem and how the waterbody is to be used.

Herbicides and harvesting should no longer be considered cosmetic treatments or quick fixes. They both have immediate, short-term, and delayed impacts. Plants and animals, including beneficial species, are poisoned by herbicides and removed by harvesting. Macrophytes regrow, but community composition and nutrient recycling are often changed. Delayed impacts occur from loss of habitat and changes in predation pathways. Disappearances of certain zooplankton, insects, and water birds can go unnoticed or appear unrelated to treatments applied months or years earlier.

Treating all or most vegetation is rarely desirable. Managers need to work with an informed public to plan when and where treatments take place (Engel 1989). For example, avoid spawning areas and times when waterfowl congregate. Native pondweed beds should usually not be treated. Bays and inshore areas need to be reserved as habitat (**CONSERVANCY ZONES**).

A treatment strategy can be developed that integrates different plant-control methods. Removable bottom screens (Engel 1984), partial winter drawdown (Nichols et al. 1988), and spot dredging (Engel and Valvassori 1989) could replace herbicide use in knee-deep water. Some areas need to be cleared for boaters; others, channeled for anglers. Separating treatment by lake use can be a strategy itself (Engel 1987b, 1989).

Consider integrating these techniques in novel ways. Harvesting can remove nuisance canopy growth that could keep 2, 4-D granules from reaching lower stems and roots of beneficial plants (Cooke et al. 1986). Take advantage of nutrient release from herbicide-killed foliage by planting desirable species (Engel 1988b, Miller 1988). Harvest

both macrophytes and rough fish to remove enough nutrients to retard algal blooms. Use herbicides or harvesting to remove plant cover and expose fry to predation, improving survival of large zooplankton that could crop phytoplankton.

Among thousands of Midwestern lakes with excessive plant growth, which should be treated? A state or regional lake classification system can establish criteria for selecting treatment sites. A three-tiered (triage) system would help by separating lakes into 3 categories: those needing no treatment, those with plant beds valued as habitat, and those needing plant control to improve recreation.

Thoughtful planning, integrating several techniques, and using them wisely can improve plant control without harming ecosystems. Herbicides and harvesting need not be weapons of destruction but tools to build more useful and diverse ecosystems.

*O, then we bring forth weeds,
When our quick minds lie still.*

*Shakespeare, Antony and
Cleopatra 1.2.113-14*

SUMMARY

Macrophyte Community Dynamics

1. Macrophyte communities reshape the physical environment by intercepting water movements and sunlight. The plants trap particles in runoff, retard bank erosion, stabilize sediment, and stratify water temperature.

2. Photosynthesis and respiration of dense macrophytes alter dissolved oxygen, carbon dioxide, pH, and alkalinity levels in lake water. During the day, pH increases and marl deposits form in hard water; at night, dissolved

oxygen decreases and kills or drives away invertebrates.

3. Macrophytes extract nutrients and heavy metals from lake water and sediment. Plant decay releases nutrients to the water and contributes organic matter to the sediment.

4. Bacteria, algae, and invertebrates inhabit macrophytes and underlying sediment. They benefit both when macrophytes grow and decay.

5. Plant beds shelter fry and exclude older fish. Stunted panfish and slow growth of game fish can result from dense foliage.

6. Macrophytes enrich plankton communities when inshore species wash into open water. Macrophyte control

would reduce this pond plankton.

7. Waterfowl need submerged macrophytes for food. They consume seeds, tubers, foliage, and plant-dwelling invertebrates.

Ecosystem Responses

1. Submerged macrophytes create microhabitats that expand food chains and establish complex food webs. These function as negative feedback loops to dampen ecosystem disturbances.

2. Dominance by Eurasian water milfoil or elodea can produce monotypic beds with long growing seasons.

3. Ecosystems respond quickly or hesitantly to disturbances. Immediate responses are short lived, but others last weeks and even years.

4. Loss of native foliage can alter species dominance in macrophyte and plankton communities, eliminate plant-dwelling invertebrates, and expose fry to predation by other fish.

5. Excessive macrophyte growth, algal blooms, or fish kills resulting from treatment hinders lake use and tourism.

Macrophyte Control

1. Herbicides and harvesting have lethal and sublethal effects. They not only kill or remove plants and animals, but also can modify the composition of ecosystems.

2. Herbicides destroy fish and invertebrate habitat. Decaying plants release nutrients that can stimulate algae and lower dissolved oxygen concentrations in lake water and sediment.

3. Harvesting removes fish and invertebrates with foliage, frightens away

water birds, and alters feeding on plankton.

4. Some macrophytes, such as chara and curly-leaf pondweed, can dominate after treatment because they are resistant to many herbicides and mechanical harvesting.

5. Herbicides and harvesting can be used creatively to improve lake use and biological diversity. Managers, working with the public, need to plan integrated programs that consider ecosystem responses to macrophyte control.

GLOSSARY

ADSORPTION - adhering of one substance to the surface of another, such as phosphates to carbonate particles in suspension, as opposed to **absorption** in which one substance permeates another.

ALKALINITY - amount of base in solution (usually carbonates, bicarbonates, or hydroxides) that can neutralize acids and thus increase pH.

BENTHOS - an organism or group of organisms that lives on the bottom, macrophytes, or objects attached to the bottom.

BIOASSAY - a technique to measure treatment effects on test organisms using controlled conditions.

BIOENERGETICS MODEL - a mathematical description of food energy transfer in an ecosystem; it might describe how many calories herbivores ingest.

BIOMASS - total weight of living organisms in an area, such as the amount of foliage and roots in a lake.

CHLOROPLAST - a membrane-enclosed structure containing chlorophyll and found usually in green plant cells.

CONSERVANCY ZONE - a space reserved for animal or plant life.

DETRITUS - organic and inorganic remains of organisms suspended in water or settled on the bottom of a water body.

ECOSYSTEM - ecological system; the physical and chemical environment linked to biological communities through energy and material transfer.

FOOD WEB - interlocking food chains, depicting transfer of food energy in an ecosystem.

FREE CARBON DIOXIDE - carbon dioxide, usually dissolved in water and uncombined with such metals as calcium or magnesium.

INVERTEBRATE - an animal without a backbone, including a rotifer, crustacean, or insect.

LITTORAL ZONE - inshore water occupied by attached plants.

MACROPHYTE - a macroscopic plant, including flowering plants (angiosperms) and macroscopic algae, such as chara.

MARL - deposits of calcium or magnesium carbonate, formed when hard water agitates or photosynthesizing plants raise the pH of lake water.

MICROCLIMATE - a local, uniform climate in a restricted area; for example, the cool shade under a water lily pad.

MICROHABITAT - an area within a larger region having a unique physical or chemical makeup, such as the blade of a macrophyte leaf.

NEGATIVE FEEDBACK LOOP - an action that triggers a counter-reaction, such as an increase of prey later reduced by predators.

PELAGIC ZONE - open water beyond reach of attached plants.

PHYTOPLANKTON - plant plankton; microscopic plants free in the water column.

PLANKTON - bacteria and small plants and animals freely floating in the water.

POSITIVE FEEDBACK LOOP - a reaction that triggers a response causing more of the same reaction; for example, an algal bloom that keeps increasing because more algal cells are produced to divide.

PROPAGULES - seeds, tubers, resting buds, or other parts that help plants disperse, multiply, or resist weather.

REDUCING CONDITIONS - a chemical environment, usually without free oxygen, that contains substances able to donate hydrogen or electrons.

RHIZOME - a horizontal underground stem, often containing tubers for food storage and nodes to sprout new shoots.

RUNOFF - water, particles, and dissolved substances that enter lakes from land or stream.

TROPHIC CASCADE - a change in predation that triggers a series of changes in herbivore and plant populations; for instance, loss of fry permits more zooplankton to survive and crop algae.

TROPHIC LEVELS - a feeding position within an ecosystem consisting of organisms, such as plants or plant-eating animals, that share a common mode of nutrition.

ZOOPLANKTON - animal plankton; microscopic animals free in the water column.

APPENDIX

Scientific names of aquatic plants mentioned in text.

Text Name	Scientific Name
coontail	<i>Ceratophyllum demersum</i>
chara, stoneworts	<i>Chara</i> spp.
curly-leaf pondweed	<i>Potamogeton crispus</i>
elodea	<i>Elodea canadensis</i>
Eurasian water milfoil	<i>Myriophyllum spicatum</i>
horned pondweed	<i>Zannichellia palustris</i>
naiads	<i>Najas</i> spp.
pondweeds	<i>Potamogeton</i> spp.
quillworts	<i>Isoetes</i> spp.
water crowfoot	<i>Ranunculus fluitans</i>
water stargrass	<i>Heteranthera dubia</i>
wild celery	<i>Vallisneria americana</i>
wild rice	<i>Zizania aquatica</i>

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Dedication

I dedicate this Bulletin to lake managers who emphasize an ecosystem approach to lake and watershed management.

Acknowledgments

This work began on invitation from Edward A. Jepsen to help evaluate the Aquatic Nuisance Control program of the Wisconsin Department of Natural Resources (DNR). This led to my March 1987 report, *Aquatic Nuisance Control (ANC) program environmental assessment. II. Affected environment. A. Factors or processes affected by ANC practices*, with introduction by Ronald H. Martin. DNR lake managers who anonymously reviewed an early draft, as well as those named below, encouraged me to rewrite it more clearly, simply, and jargon-free. And so this Technical Bulletin was written.

Information on harvesting impacts came partly from my 1985 study of harvester operations in Wisconsin, while I was assigned to the DNR's Lake Management Program of the Bureau of Water Resources Management.

I thank Dr. James F. Kitchell, Cynthia C. Lunte, and Dr. Craig S. Smith of the University of Wisconsin-Madison for reviewing an earlier revised draft. Robert T. Dumke and Richard B. Kahl of the DNR reviewed the pages on waterfowl. Thomas M. Bainbridge, Frank J. Koshere, and Patrick W. (Buzz) Sorge of the DNR evaluated the manuscript's readability from a lake manager's perspective. Douglas R. Knauer of the DNR and Dr. Stanley A. Nichols of the Wisconsin Geological and Natural History Survey reviewed both early and final drafts. Bureau directors in DNR's Division of Resource Management provided administrative approval.

For using their photographs, I thank Douglas W. Stamm (ProPhoto, Sauk City, WI) and DNR staffers Thomas M. Bainbridge, Gerald A. Bartelt, Richard B. Kahl, Richard A. Lillie, David W. Marshall, Carl R. Molter, Timothy A. Rasman, and Wendell J. Wojner.

About the Author

Sandy Engel trained in fish ecology and limnology at Indiana University and the University of Wisconsin-Madison. He joined the Department in 1976 as a project leader in the Water Resources Research Section of the Bureau of Research. He has written articles and reports on fish and zooplankton ecology, macrophyte community ecology, lake-use planning, and using blankets, screens, dredges, and harvesters to control aquatic vegetation. He has now completed research, with Stanley A. Nichols, on restoring the macrophyte community of Rice (Glenton) Lake in Wisconsin's Polk County.

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