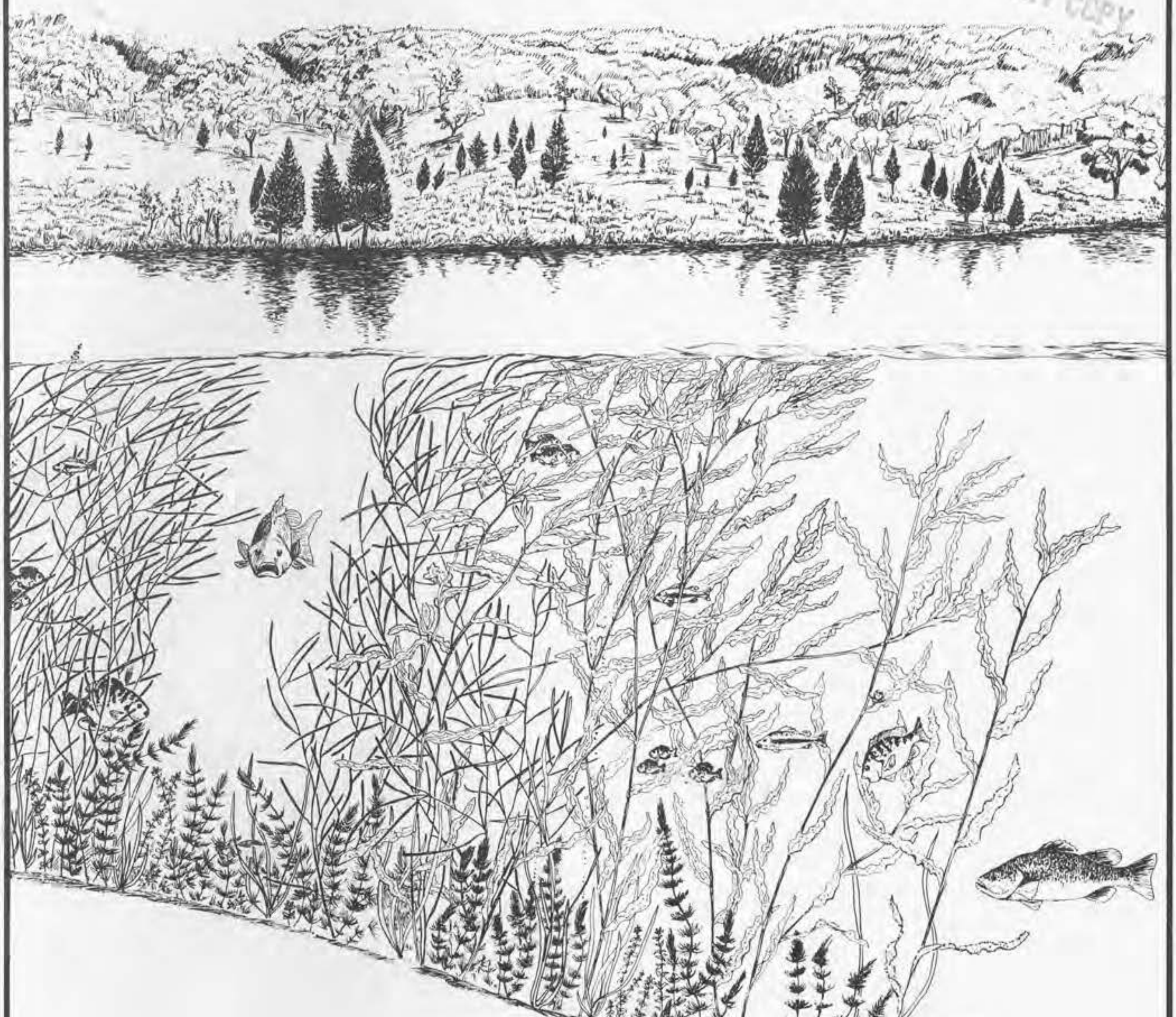
Aquatic Community Interactions of Submerged Macrophytes

Phytoplankton
Zooplankton
Macrophytes
Fishes
Benthos



Technical Bulletin No. 156
DEPARTMENT OF NATURAL RESOURCES
Madison, Wisconsin

1985

"When one tugs at a single thing in nature, he finds it attached to everything else in the world."

- John Muir

FOREWORD

Dominating the shallows of many lakes are large flowering plants. Essential as fish and waterfowl habitat, these underwater prairies are so intricately bound to the food web of lakes that eradicating them for boating or swimming has not always been successful or desirable. A comprehensive study of the ecology of macroscopic plants was needed to move forward with developing new management strategies.

This study, conducted by the DNR's Bureau of Research, details the seasonal wax and wane of plants and associated life in Halverson Lake. Nestled in Wisconsin's hilly southwest, this shallow impoundment is important not for its recreational value, but as a model to understand plant community interactions unhampered by excessive runoff, pesticides, speed boating, and other disturbances. Frequent reference to relevant literature on aquatic plants broadens the base of the study.

This treatise forms the core of several publications dealing with innovative approaches to plant management. Drawdown and bottom blanketing, removable screening, and mechanical harvesting are subjects of previous works by the author. Forthcoming articles will detail (1) impacts of harvesting lake vegetation on Halverson Lake, (2) mechanical harvesting programs in Wisconsin, and (3) creative lake-use plans for managing with macrophytes. The latter is introduced in the concluding section of the present work.

I hope that this technical bulletin will ultimately serve lake managers as a useful reference source for information and ideas on macrophytes and their ecology.

Kent E. Klepinger
October 1985

ABSTRACT

The community structure and interactions of submerged macrophytes were examined from 1977 through 1983 in Halverson Lake, a shallow 4-ha (10-acre) impoundment in southwestern Wisconsin.

Divers sampled macrophytes along transects; an Ekman dredge, suspended multiple-plate samplers, and plant nets gathered macroinvertebrates; fishes were boom shocked; and plankton were vertically collected with a net or Kemmerer sampler.

Vascular plants covered 40-70% of the bottom in June-August, stratified vertically into three layers, and spread in zones to a depth of 3.5 m (11.5 ft). Standing crop reached 130-200 g/m^2 (dry weight) in July and consisted mostly of Berchtold's, curly-leaf, and sago pondweeds (*Potamogeton* spp.), coontail (*Ceratophyllum demersum* L.), and water stargrass (*Heteranthera dubia* (Jacq.)).

Macroinvertebrates congregated on or beneath macrophytes, where they were grazed by bluegills (*Lepomis macrochirus* Raf.) and largemouth bass (*Micropterus salmoides* (Lacepède)). Bluegills also consumed macrophytes. Black crappies (*Pomoxis nigromaculatus* (Lesueur)) ate zooplankton offshore. Rotifers dominated the net zooplankton. Blue-green algae amassed after June, in response to nutrient runoff and macrophyte decay.

Submerged macrophytes functioned to create microhabitats and microclimates inshore, selectively shelter fishes and their prey, replenish detritus and benthic algae eaten by invertebrates, diversify the zooplankton, and improve water clarity by stabilizing sediments and storing nutrients.

AQUATIC COMMUNITY INTERACTIONS OF SUBMERGED MACROPHYTES

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Technical Bulletin No. 156
DEPARTMENT OF NATURAL RESOURCES
P.O. Box 7921
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1985

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INTRODUCTION

The shallows of lakes, clear and densely carpeted with summer plants, can be fascinating and mysterious. The confusion of foliage greeting a diver's descent, gives way to thoughtful contemplation of form and function, of habitat and diversity. Panfish dart among **macrophytes*** riddled with colonizing insects and snails. Busy neighborhoods from below the waves become scorned by boaters and swimmers on the water surface.

Underwater macrophytes pose a challenge to lake management. They can grow too dense or too sparse. Dense beds of macroscopic algae, mosses, stoneworts, or vascular plants (angiosperms) can impede boating, fishing, and swimming. Decomposing plants can release noxious odors, litter beaches, and remove dissolved oxygen from the water. Young fishes can grow poorly in dense vegetation, from overgrazing their food, as well as in sparse flora, from a scarcity of habitat for prey.

Attempts to eradicate nuisance vegetation belie their usefulness and relationships with other organisms. Macrophytes support a diverse community of **benthos** (Allee 1912, Krecker 1939, Rosine 1955). By intercepting runoff, storing nutrients, and stabilizing sediments, macrophytes retard algal blooms and improve water clarity (Kofoid 1903, Goulder 1969, Modlin 1970, Kogan 1972). Suddenly removing macrophyte beds could reduce water clarity, force fishes to graze zooplankton offshore, and stimulate phytoplankton blooms from the unstored nutrients and reduced pressure of invertebrate predation. Widespread ecosystem changes can result from unwittingly removing macrophyte beds.

This study aimed to determine how the macrophyte community of a Wisconsin lake (1) is organized, (2) changes seasonally and yearly, and (3) interacts with other biota. The role of submerged macrophytes in other lakes was reviewed to provide managers with a broader base of information relevant to Wisconsin. Field sampling was designed to assess the impact of submerged macrophytes on (1) macroinvertebrate composition and distribution; (2) fish activity, diet, and growth; (3) zooplankton composition and seasonal changes; and (4) phytoplankton blooms, primary productivity, and water clarity. These interactions were further evaluated by harvesting 30-70% of the vegetation midway through the study.

The study originated from widespread concern about underwater macrophytes in lakes, an extensive literature search, and recommendations by management staff in a 1976 Departmental survey (Research Advisory Council Report to the Natural Resources Board, "Programs, Problems and Research Needs in Water Resources Research").

STUDY AREA

Halverson Lake, Iowa County, Wisconsin was selected as a research site because it has extensive vegetation in summer, yet contains no carp (*Cyprinus carpio* L.) that uproot plants and create turbidity, never winterkills, receives little public use, has never been treated with plant or fish toxins, and allows access to a plant harvester (Engel 1979). Absence of these interfering factors would permit the broadest application of research findings.

Halverson Lake was built as a private fish hatchery in 1959 by damming a headwater branch of Mill Creek, a north flowing tributary of the Wisconsin River. It is located in Governor Dodge State Park, in the steep unglaciated driftless area, and drains into Twin Valley Lake. Surrounding ridges tower 14-66 m above the lake surface. The drainage basin of about 250 ha is over 80% covered with woods and grassy fields in secondary succession (Table 1). The fields were pastured and lightly cropped before the lake was built, but are now undeveloped.

Surrounding soils range from poorly drained silty loams (Etrick and some Fayette series) near the lake to more permeable sandy soils (Dubuque and Fayette series) on upland slopes (Klingelhoets 1962). The soils have been eroded from sandstone slopes and limestone bluffs. They are underlain by a bedrock of Cambrian sandstone and Galena dolomite, yielding ground water of moderate but varying hardness. The lake bottom consists of dark organic mud and scattered patches of sand, clay, and marl.

The lake and adjoining wetlands form a ground water discharge unit. Springs upwell on the lake bottom. Two permanent streams arise from upland springs and enter the north end of the lake. Temporary streams flow to the lake after snow melt in March and heavy rains in summer. Wetlands of Type II inland fresh meadows (Shaw and Fredine 1956) and nine upland ponds (less than 0.3 ha) intercept these stream flows. They function as settling basins to reduce lake turbidity. Lake water level is set by a drop inlet structure at the dam (Linde 1969).

TABLE 1. *The Halverson Lake drainage basin.*[a]

Land Use	Area (%)
Woods	48
Dry fields	38
Croplands	5
Wetlands	4
Roads	2
Halverson Lake	1.4
Upland ponds	0.9

[a] Total area = 250 ha.

* All terms defined in the glossary are shown in **bold face** type the first time they are used in the text.

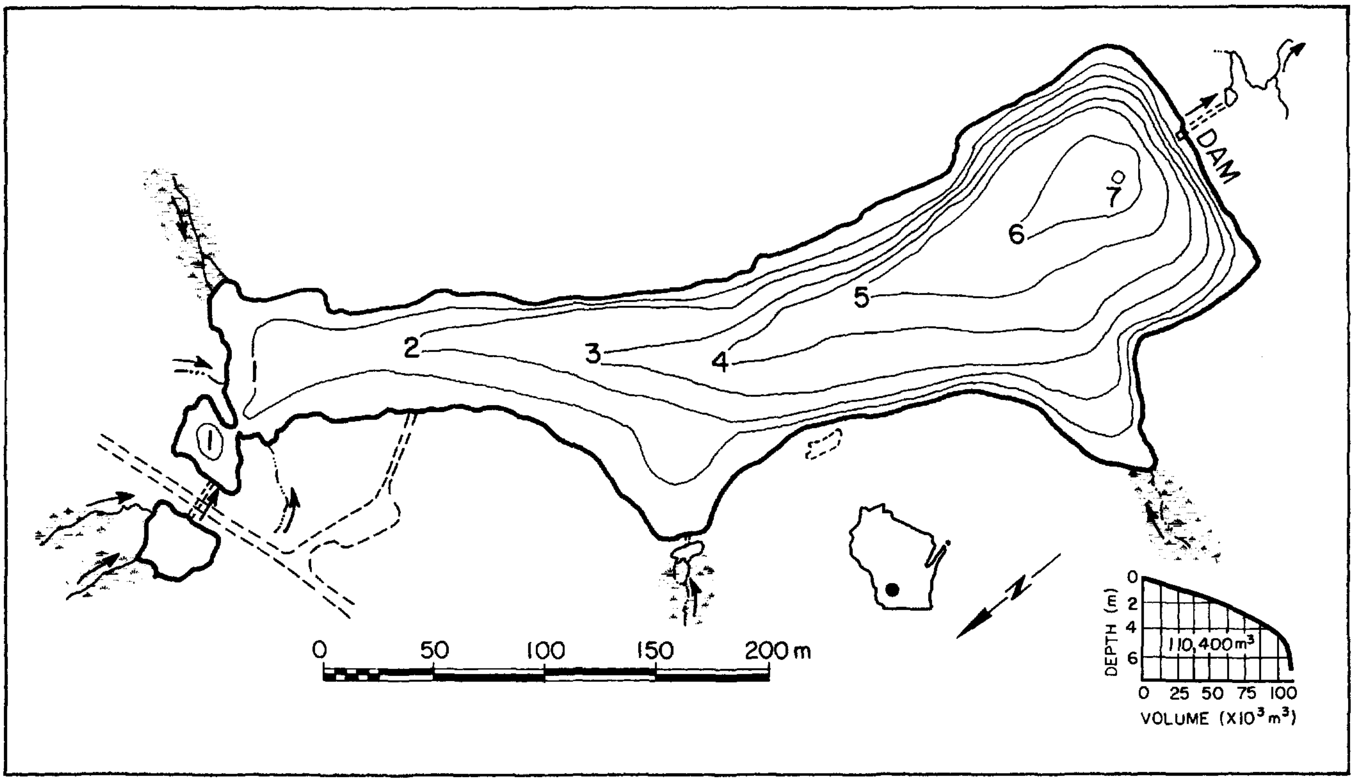

FIGURE 1. *Bathymetric map of Halverson Lake, sounded in 1978 and 1979.*

TABLE 2. *Morphometry of Halverson Lake.*[a]

Parameter	Distance (m)
Shoreline length	1,440
Maximum total length	504
Maximum wind fetch	469
Maximum width	190
Mean width	90
Maximum depth	7
Mean depth	2.6
Relative depth (%)	3.1
Surface area (ha)	4.2
Shoreline development	1.99
Volume development	1.12
Total volume (m^3)	110,400

[a] Terminology and calculations follow Welch (1948).

The lake basin has an elongated dendritic shape, with several shallow bays, reflecting the confluence of former stream channels (Fig. 1). The basin covers 4.2 ha, averages 2.6 m deep, and increases in depth to 7 m before the dam (Table 2). About 45% of the lake volume lies within 1.5 m of the water surface, the depth limit of many plant harvesters. A thermocline forms in summer from 3.5 m to the bottom, leaving 80% of the open water homoiothermal and mixed.

Epilimnetic water has a mean total hardness of 130-190 mg $CaCO_3$/L, total alkalinity of 120-180 mg $CaCO_3$/L, pH of 7.4-8.6, and total phosphorus of 20-60 µg P/L. Dissolved oxygen becomes depleted below 4 m in summer and winter.

Bluegills (*Lepomis macrochirus* Raf.), black crappies (*Pomoxis nigromaculatus* (Lesueur)), and largemouth bass (*Micropterus salmoides* (Lacepède)) were stocked in 1959-60 (M. Halverson, pers. comm.). Motor trolling is prohibited and only battery-powered electric motors are allowed on the lake. Anglers mostly fish from shore. Lake use is discouraged by absence of an improved boat access, remote location of the lake in the 2,000-ha park, and presence of two larger reservoirs nearby for bathing and boating.

METHODS

Macrophytes

Biomass. Submerged and floating macrophytes were sampled in August 1977 and June, July, and August 1978 through 1982. Nearly 1,400 plant biomass samples were collected on 20 dates using a stratified random design and the line-intercept method (Lind and Cottam 1969). The shoreline was first divided into 15 transect areas (Fig. 2). A transect line was randomly located within each area and floated out from shore. Divers collected samples every 5 m along the line, starting 1 m from shore (Fig. 3). The plants were gathered off the bottom with a three-sided aluminum frame, measuring 40 by 50 cm (0.2 m^2). Transect 1 circled a 0.1-ha unharvested bay; Transects 2-15 were situated around the harvested main lake. Free diving was used to take most samples; SCUBA diving assisted in deep water and to study plant distribution. Collected samples were stored in plastic bags and transported in a cooler to the laboratory.

Plants were frozen in the laboratory to permit time for other field work and later thawed, sorted to species, cleaned, and weighed. Plant samples collected in 1982, however, were processed without first freezing them. Dry weight biomass was determined by drying the plants first in air and then in a forced air or convectional oven at 105 C for 48-72 hours. Roots were not included in any biomass measurement because they usually broke off during sampling. To be consistent among samples, roots were further removed during cleaning. Rhizomes remained on the plants. Underground biomass averages less than 10% of the total dry weight biomass in summer, for submerged plant species found in the lake (Sculthorpe 1967, Schiemer and Prosser 1976).

Distribution. The horizontal distribution and depth limits of submerged macrophytes were mapped within a week of biomass sampling. Plant distribution was also mapped on three dates (27 June 1978, 1 July 1982, and 29 July 1982) when biomass samples were not collected. A metered line was stretched across the lake at numerous locations to measure the distance from shore of surface and bottom vegetation. Surface vegetation was also photographed on the ground and from an airplane using 35-mm normal color and false-color infrared films. Normal color film revealed plants to a depth of 0.7-2.5 m, depending on water clarity; infrared film delineated plant beds mainly on the water surface.

Plant depth was measured along each transect with a metered line tied to a weighted Secchi disk, to keep the line taut without it sinking into the sediments. The depth limit of plant growth was set at 1 g/m^2 dry weight (about 10 g/m^2 wet weight). Areas with a sparser plant growth looked barren underwater. This depth limit defined the offshore boundaries of plant

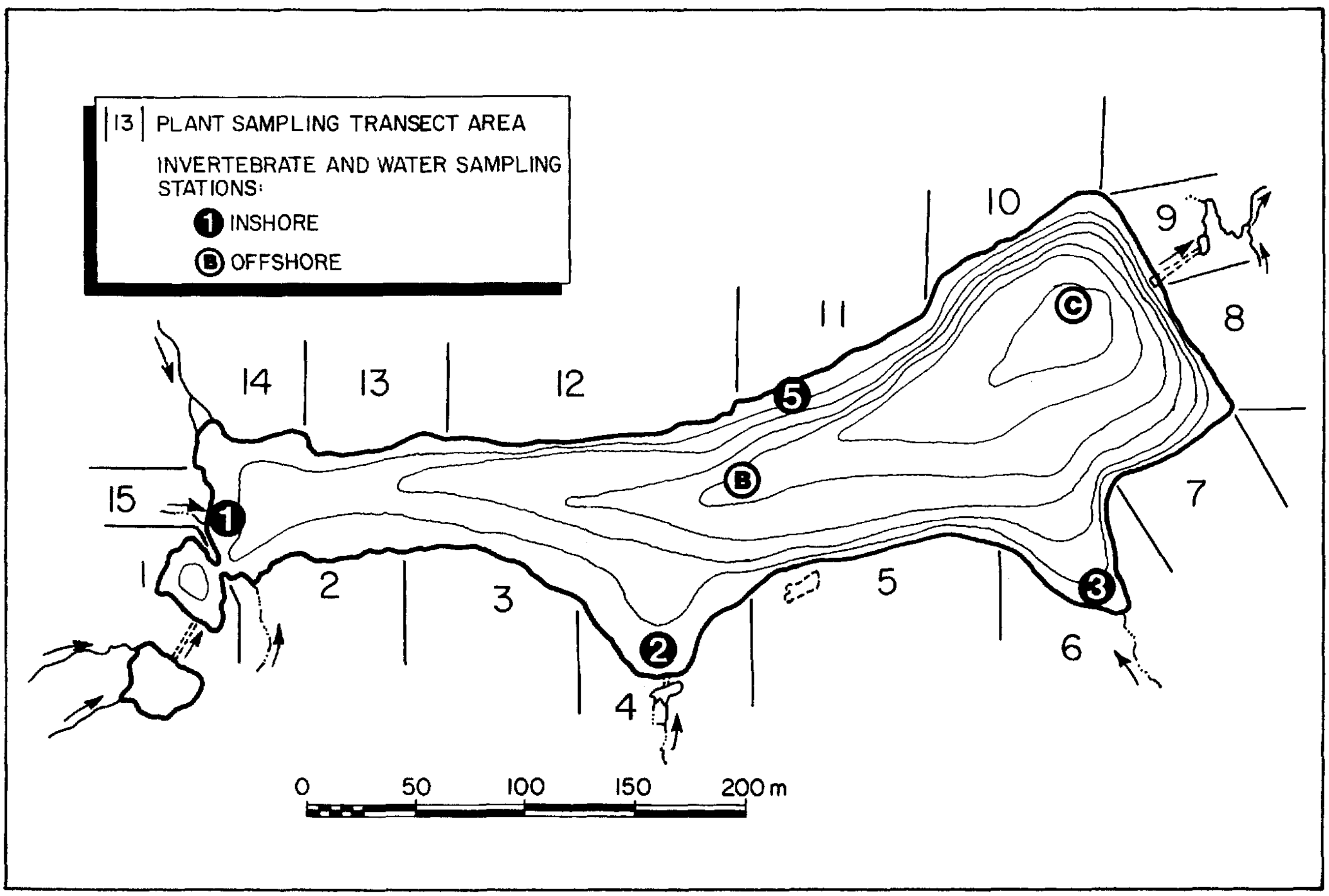

FIGURE 2. *Sampling design on Halverson Lake. Macrophyte transects are numbered outside the lake; invertebrate and water sampling stations are numbered inside the lake.*

FIGURE 3. *Sampling macrophytes every 5 m with the line-intercept method. Brian J. Andraski appears in the foreground.*

beds and avoided including single isolated plants on distribution maps.

Harvesting. Macrophytes were harvested for 2-3 days each in mid-June and mid-July 1980 and 1981. The plants were freshly weighed on a truck scale in Dodgeville and hauled to a park site away from the drainage basin, so that nutrients would not leach back into the lake. The macrophyte community was observed until August 1985 to follow changes after harvesting. A fuller account of macrophyte harvesting and its impacts is given elsewhere (Engel 1980, 1983).

Macroinvertebrates

Bottom and Multiple-plate Samplers. Macroinvertebrates were gathered on the bottom with an Ekman dredge (152 by 152 by 152 mm) and from midwater (0.5 m) with multiple-plate samplers (Fig. 4). The multiple-plate samplers were modified from Hester and Dendy (1962) by inserting construction webbing between alternate pairs of seven tempered hardboards. Three steel washers separated boards where no webbing was used. The boards measured 80 by 80 mm and were 6.4 mm thick. Boards, webbing, and washers were held together by a 100-mm steel eyed-bolt. The samplers were suspended by a line tied to an anchored floating plank. Three samplers dangled from the same plank.

The samplers remained in place for about 4 weeks. Macroinvertebrates incompletely colonized samplers left for less than 3 weeks, whereas epiphytic algae grew on samplers held much beyond 4 weeks. A long-handled dip net, with No. 20 (78 μm) mesh, was used to lift each sampler and catch organisms falling off them.

During ice-free periods, Ekman dredge and multiple-plate samples were taken every month in inshore Stations 1, 2, 3, and 5 (Fig. 2). Ekman dredge samples were also gathered once each winter and on all dates in offshore Stations B and C. Three Ekman dredge hauls were made, from different sides of the boat at each station and composited into a single sample. The three multiple-plate samplers were analyzed separately and their sample counts averaged for each station. Ekman dredge samples were collected on 41 dates from October 1977 through October 1982; multiple-plate samplers were worked on 22 dates from June 1978 through October 1981.

Ekman dredge and multiple-plate samples were preserved in the field with 75% *v/v* ethanol. As each multiple-plate sampler was removed from the lake water, it was stored in a separate plastic container with the alcohol. The samplers were later dismantled in the laboratory and the colonizing organisms were sorted with forceps and washed through a No. 30 (600 μm) mesh sieve. Ekman dredge samples were field strained through a No. 60 (250 μm) mesh sieve, then preserved, and finally restrained in the laboratory through a No. 30 mesh sieve. Although small chironomid larvae could pass through these sieves (Nalepa and Robertson 1981), few did so when the effluent from the sieving was repeatedly examined. Ostracods were lost, however, and could not be reliably counted.

Plant Nets. Plant-dwellers were collected with nets made of Nitex* mesh (363 μm) cut to 76 by 76 cm (Fig. 4). An aluminum embroidery ring of 13-cm diameter stretched the netting. Corner rings and stones anchored the nets on the bottom at a depth of 1 m. Each corner of the net was tied by a string to a 5-cm floating cork. Some nets held a clump of macrophytes; others served as controls for invertebrates colonizing the netting. Raising the corks lifted the netting around the plants to trap the organisms as the samplers were removed from the water. Plant nets were stationed among undisturbed plant beds for 8-32 days in June and July 1979-82. Nets with catch were returned unpreserved to the laboratory in separate plastic bags. Macroinvertebrates were separated from the plants and netting with a forceps and by washing through a No. 30 sieve. The plants were then cleaned, sorted to species, and oven-dried at 105 C for 48 hours. Results were expressed as number of organisms, minus those on control nets, per gram dry weight of macrophytes.

Counting Benthos. Macroinvertebrates from all samplers were either totally counted or subsampled. Total counts were made of sparse samples or some rare taxa in otherwise abundant samples. Most samples were first subsampled by spreading them onto a tray, stirring the contents, and then dividing each sample into 36 compartments with a plastic grid. Each compartment represented a subsample of equal volume. Five subsamples were

* Reference to trade names does not constitute an endorsement by the author or the Wisconsin Department of Natural Resources.

randomly selected for counting. Nine subsamples (25% of the sample) were counted if the counts of the first five subsamples exceeded 50% of the median for these counts. A dissecting microscope, with a total magnification of 14-66X, was used to identify, sort, and count all organisms. Some samples were stained with rose bengal to help sort the organisms from debris (Williams and Williams 1974).

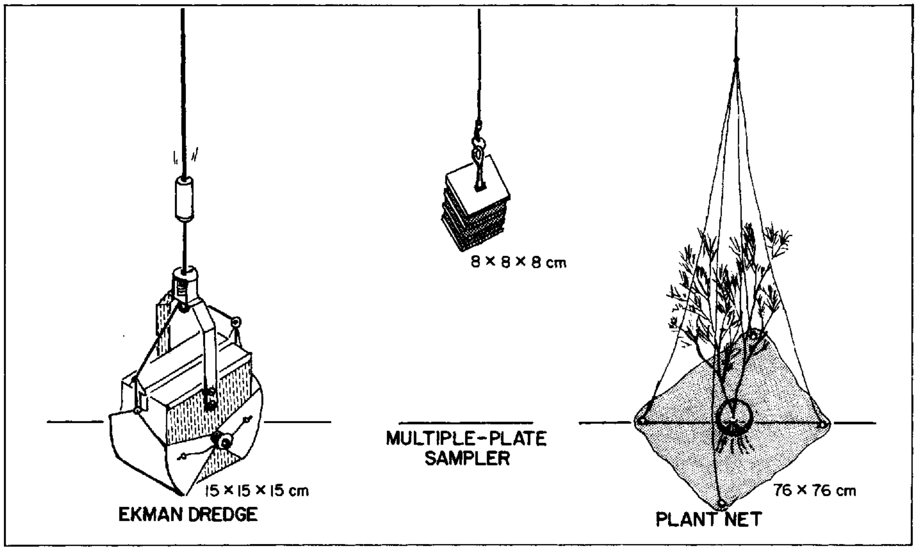

FIGURE 4. *Macroinvertebrate samplers used in Halverson Lake. The lake bottom appears as a horizontal line. The samplers are not drawn to the same scale.*

Fishes

Fishes were electrofished with a 4.7-m boat every few weeks from April to November. Most samples were collected during the day. An AC-pulsed DC generator delivered an electrical output of 280-300 V and 6 total A at 60-80 Hz and 25% pulse rate. This system was replaced after June 1978 with an AC generator producing about 210 V and 6-9 A. Specific conductance of the lake water exceeded 150 S/cm (corrected to 25 C). Boom shocking was effective to a water depth of nearly 2 m.

Diet. Stomach contents of 5-30 fishes of each species were examined every sampling date. Fishes under 150 mm total length were dissected. Larger fishes had their stomach contents flushed into a plankton net by pulsed gastric lavage (Foster 1977), given a partial pectoral fin clip to follow survival, and released. Stomach contents were preserved in 5% *v/v* formaldehyde. Flushing evacuated 98-100% of all foods, when tested on 18 bass and 8 crappies dissected after flushing. Foster (1977) and Light et al. (1983) obtained similar flushing efficiencies and found the method more effective than traditional stomach pumping (Seaburg 1957).

The total volume of food in each stomach was measured by water displacement. Food was added to water in a calibrated centrifuge tube. The displaced water was transferred by glass syringe and tubing to a buret (± 0.01 ml), where the displaced volume was measured.

Prey were then sorted, identified, and counted. *Daphnia* and chironomid larvae were randomly subsampled when too numerous to totally count. Plant matter was measured for volume rather than counted.

Percent occurrence (percentage of stomachs with each food category, excluding empty stomachs), relative abundance (percent of the total number of food items counted), and mean number/stomach (including empty stomachs) were tallied for each food category. Percent occurrence (O_i) and relative abundance (P_i) were combined into a relative importance index (RI) for each ith food category (modified from George and Hadley 1979):

$$RI = (O_i + P_i) / \sum_i (O_i + P_i)$$

Index values range from 0 to 100. They deflate the contribution of abundant items eaten by few fishes and magnify that of rare foods consumed by many fishes.

Percent of food overlap between fish species was calculated from Schoener (1970):

$$S = 100 - 0.5 \sum_i (P_{xi} - P_{yi})$$

where P_{xi} and P_{yi} are percentages of the ith food category consumed by fish species x and y. The measure ranges from 0% to 100%. It was calculated on each sampling date when at least 5 fish of each species was captured. Abrams (1980, 1982) and Mittelbach (1984) justified its usefulness in niche overlap studies.

Food selection by crappies on pelagic microcrustaceans was measured by Ivlev's (1961) electivity index (E):

$$E = (R_i - P_i) / (R_i + P_i)$$

where R_i is the percentage of the ith zooplankton species in crappie stomachs and P_i is the percentage of the same species in the lake. E values range from -1 (complete avoidance or inaccessibility of prey), through 0 (no selection or random feeding), to +1 (complete selection or preference). The index was used to measure selection on common zooplankton species, since the accidental ingestion of a zooplankton species absent from lake samples would yield an E value of +1. Dodson (1970) and Strauss (1979) review the merits of the index.

Calculations were based on daytime samples of fishes and plankton. Zooplankton counts were averaged for Stations B and C, after deleting nauplii and rotifers as too small to be prey. *Chaoborus* larvae were also eliminated, since crappies probably ate them in the evening as the larvae were moving off the bottom.

Growth, Age, and Standing Crop. The growth of live unmarked fishes, randomly selected from larger electrofishing catches, was measured each August or October. Each fish was measured for total length (± 1 mm) and weighed (± 1-2 g for fishes weighing 0-1,100 g.; ± 25 g for larger fishes). A regression equation for length (L) and weight (W) was calculated for each sample:

$$\log W_i = \log a + b\,(\log L_i)$$

where the constants, a and b, represent the y-intercept (a) of weight (y-axis) and length (x-axis) and the slope (b). When b drops below 3.0, fish appear thinner with increasing length; when it goes above 3.0, they appear heavier as they grow (Tesch 1968).

Relative plumpness of each fish was assessed by the condition factor (K) (Lagler 1956):

$$K = (W_i / L_i^{3.0}) \cdot 10^5$$

The regression slope (b) was assumed to be 3.0 to compare samples and studies. Condition factors must be cautiously interpreted, since they vary among fish species and change as body shape and density are altered during growth and spawning (Carlander

1977). They are most relevant for comparing samples of similar age composition.

Fishes were aged by pressing scales onto acetate strips (Smith 1954). They were removed just ventral to the lateral line and posterior to the pectoral fin. True and false annuli were identified by criteria in Sprugel (1953) and Regier (1962). At least three scales from each fish were aged independently by several persons. Troublesome scales (less than 10%) were re-examined after several months or sent to outside investigators for aging. Separate ages were not assigned to most bluegills above scale age V, or bass over age VI, because the crowded annuli were difficult to count.

Standing crop was measured by mark/recapture, using the Bailey-modified Petersen formula (Ricker 1975). Fishes were marked by clipping the lower tip of the tail, held for a few days in live boxes to cull dead ones, and released throughout the lake to ensure random mixing with unmarked fishes. Large bass were not held after marking, to avoid predation in the live boxes. Fishes were marked in August 1977 or October 1978-82 and recaptured after 1-3 weeks.

Population size of each species was calculated by adding separate estimates of several size classes. Every fish was measured for total length. Every fish 125 mm and over in length, and every tenth fish under this size, was also weighed and aged from scales. Fishes under 50 mm (mostly age 0 bluegills) could not be effectively caught and were eliminated from the census. Annual standing crop was then calculated for each size class by multiplying the estimated number of fish by their mean fresh weight.

Zooplankton

Zooplankton were collected around noon (CST) with a conical net having a length of 710 mm, a mouth diameter of 155 mm, and a mesh of No. 20 (78 μm) Nitex. The net was hauled to the water surface from 0.5 m above the lake bottom for a distance of 3.5 m at Station B and 5.5 m at Station C. It was retrieved slowly and steadily to reduce water turbulence across the net opening.

This method underestimates the number of protozoans and some rotifers (Likens and Gilbert 1970, Pace and Orcutt 1981) and can lead to net clogging. The latter only became evident when blue-green algae appeared in summer and then mainly occurred at the end of tows.

Samples were preserved in the field with 2-3% *v/v* neutralized formaldehyde. They were later concentrated by settling in graduated cylinders. Most species were counted in a Sedgewick-Rafter cell under a compound microscope (100X total magnification). Several random subsamples were drawn with a 1-ml Hensen-Stempel pipet (Edmondson 1971). Sparse winter samples and occasionally small species in other samples did not distribute randomly and had to be totally counted. Total counts were often made of ostracods and *Daphnia* and always made of insect larvae, *Leptodora*, and water mites using a petri dish under a dissecting microscope (14-66X). Nauplii were separated into calanoids and cyclopoids, but copepodids were identified to species and counted as separate instars from characters in Torke (1974) and Czaika (1982).

Phytoplankton

Water was collected every few weeks (except once in winter) at depths of 0.5, 1.5, 2.5, and 3.5 m with an opaque Kemmerer sampler. Cell counts and biovolumes were determined from a sample mixed equally from all depths at Station C and preserved with 2-3% *v/v* acid Lugol's solution. Chlorophyll and productivity were analyzed separately from each depth at Stations B and C. These samples were returned to the laboratory under ice and filtered the next day, under 300 mm Hg pressure, through a cellulose triacetate filter (Gelman GA-6 of 47-mm diameter and 0.45-μm mesh).

Cell Count and Biovolume. Samples were settled for at least 48 hours onto combined plate chambers of 10-cm height (Hasle 1978). Cells were then counted by the Utermöhl method (Lund et al. 1958), using a phase-contrast inverted microscope fitted with an ocular micrometer ruled into fields. Cells were counted at total magnifications of 560X or 1,400X. Two 50-ml aliquots and 40 random fields were counted for most samples; 100-ml aliquots and 120 fields had to be counted for sparse winter samples. Cell counts of *Anabaena* and *Microcystis* were based on mean cell number of random filaments or colonies.

The biovolume of each taxon was estimated by fitting mean cell size to a volume formula approximating cell shape (Rott 1981).

Chlorophyll. Filtered chlorophyll was extracted with 5 ml of 90% acetone and 10% $MgCO_3$ for several days in a freezer. Cells were pulverized with an electric tissue grinder and centrifuged at 1,500 rpm (1,100 gr). Trichromatic chlorophyll-*a* was measured at 663 nm; monochromatic values were measured at 665 nm within 1-2 min of adding 1N HCl (Weber 1973). Turbidity was corrected by subtracting the absorption at 750 nm, measured before and after acidifying. Absorptions were determined with a Bausch and Lomb (Spectronic 70) spectrophotometer (10-mm path length). With an 8-nm slit width, the unit recovered 80-92% of the chlorophyll. Absorption at each wave length was corrected by comparing the Spectronic 70 with a Perkin-Elmer (models 124D or 200) spectrophotometer (0.5-nm slit width) at the State Laboratory of Hygiene, Madison, Wisconsin. Comparisons were made with quality control samples of chlorophyll, prepared by the U.S. Environmental Protection Agency, Cincinnati, Ohio.

Values reported as chlorophyll are monochromatic chlorophyll-*a*, unless otherwise stated.

Productivity. Primary productivity was measured *in situ* for 4 hours, centered at noon (CST), using three clear and one opaque BOD bottle (300 ml) at each depth (Vollenweider 1969). Samples were injected with 0.60 ml $NaH^{14}CO_3$ (10.0 μCi/ml) using a syringe. Photosynthesis was arrested after incubation by placing the samples under ice in the dark. Respiration was inhibited with 1 ml/sample of 1% *w/v* sodium merthiolate.

After filtering 100 ml of sample (300 ml in winter), the algae were added to 15 ml fluor, prepared from 100 g naphthalene, 7 g PPO (2,3-diphenyloxazole), and 0.3 g POPOP (1,4-phenyloxazoly benzene) added to 1 liter 1,4-dioxane. Fluor samples were counted by liquid scintillation using a Packard Tri-Carb (model 3324) scintillation counter. Sample counts were corrected for quenching and counter efficiency using quench standards and the channels ratio method (Herberg 1965). The activity of ^{14}C added to each sample was assayed on each date with five unfiltered samples of deionized water inoculated in the field.

Productivity was calculated by subtracting the dark bottle activity from the median activity of the three clear bottles. Values lie between gross and net productivity, due to carbon losses from photorespiration (Peterson 1980). Productivity may have been underestimated, because dark carbon dioxide fixation was not corrected (Legendre et al. 1983). A $^{14}C/^{12}C$ uptake ratio of 1.05 was assumed (Vollenweider 1969). Total inorganic carbon in the lake water was calculated from water temperature, pH, and total alkalinity titrated to pH 4.5 with a pH meter.

Water Quality

Water temperature, transparency, and chemistry were measured when sampling plankton. Water temperature was recorded at every 0.5-m depth with an electric thermistor. Transparency was judged by two persons from the shaded side of an anchored boat with a 20-cm Secchi disk, painted black and white (Welch 1948). The two readings were averaged for each station.

Water chemistry samples were collected at each 1-m depth with an opaque Kemmerer sampler. They were returned to the Nevin Hatchery under ice in a dark cooler, and analyzed the next day for dissolved oxygen with the azide-modified Winkler method, pH and total alkalinity (to pH 4.5) with a glass electrode and pH meter, and total hardness with the EDTA method (American Public Health Association 1976). The titrating solutions were standardized twice on each date to correct for changes in normality. Dissolved (true) color was measured with a Hellige Aqua Tester (model 611A) after filtering the water through a 0.45-µm membrane filter. Specific conductance (corrected to 25 C) was determined with a Wheatstone bridge.

Nitrogen and phosphorus were analyzed after March 1980 by the State Laboratory of Hygiene. Unpreserved samples were collected at 0.5-, 3.5-, and 5.5-m depths, refrigerated overnight, and analyzed the next day for inorganic N (colorimetric brucine sulfate), organic N + NH_4^+ (Kjeldahl digestion), total N (sum of all nitrogens), and total P (persulfate digestion), mostly following U.S. Environmental Protection Agency (1979).

Diversity and Statistical Analysis

Sample diversity was calculated as Shannon and Weaver's (1949) index:

$$H = -\sum_{i}^{n} P_1 \log_2 P_i$$

where P_i is the proportion of individuals in the ith taxon. Ranging from 0 to infinity, the index increases with the number of taxa (n) and becomes maximum when the taxa are equally proportioned in the sample. The maximum diversity is simply the $\log_2 n$. Percent evenness calculated how close sample diversity approaches maximum:

$$\% \text{ evenness} = \frac{\text{sample } H}{\text{maximum } H} \cdot 100$$

Since all taxa in a community must be known, the index can only approximate diversity for small samples (Pielou 1975).

Sample diversity, product-moment correlation coefficients, regression equations, t-tests, and one-way ANOVA were calculated with Minitab computer programs (Ryan et al. 1981). Probabilities calculated for the test statistics were considered significant for $P < 0.05$ and highly significant for $P < 0.01$.

Sample averages were reported as mean $\pm$ 1 SE unless otherwise stated. Means of chlorophyll and productivity were weighted for volume differences in sample depth.

RESULTS AND DISCUSSION

MACROPHYTE COMMUNITY STRUCTURE

Taxa

The community of submerged and floating macrophytes comprised 19 species, including 13 angiosperms, 4 filamentous macroalgae, and 2 stoneworts (Table 3). Cladophora and spirogyra were the most common filamentous algae found inshore. Chara and nitella were the only stoneworts identified from the lake. Most of the macrophytes, including emergent species, were monocots. Coontail, northern water milfoil, and water smartweed were the only dicotyledonous plants found. Most macrophytes occurred every year of the study. Oedogonium, wild celery, and water smartweed were rare and identified only from a few specimens. Only curly-leaf pondweed was not native to North America (Fassett 1966).

The macrophytes of Halverson Lake were typical of hard water lakes with soft bottoms. They occurred in many Wisconsin lakes visited during the study and were listed by others (Belonger 1969, Modlin 1970, Nichols 1974, Richardson 1974). Pondweeds dominated the community in most years, especially sago pondweed, Berchtold's pondweed, and curly-leaf pondweed. I first identified Berchtold's pondweed as small pondweed from Fassett (1966). Its leaf morphology was so variable that it was best to synonymize it with Berchtold's pondweed, following Voss (1972).

Some species of macrophytes were conspicuously absent from Halverson Lake. Bladderwort (*Utricularia* spp.), broad-leaved pondweeds (*Potamogeton* spp.), Eurasian water milfoil (*Myriophyllum spicatum* L.), water lilies (Nymphaeaceae), and watermeal (*Wolffia* sp.) occurred on nearby lakes, but were not located on Halverson Lake. Only lesser duckweed and filamentous algae comprised the freely floating species (**epipleuston**) on the lake. The upstream location of Halverson Lake, its restricted access to boats (which could carry plants), low public use, and presence of a dense previously undisturbed macrophyte community partly insulated the lake against plant introductions.

Nine species of emergent macrophytes grew at the lake shore (Table 4). They extended into the sedge meadows that partly surrounded the lake and its inflowing streams. The plants comprised the upper littoral and **eulittoral zones** (Wetzel 1983). Roots and crowns usually remained submerged to a depth of about 0.3 m. Cattails extended about 5 m from shore at Transect 6, but it and other species remained within a meter of shore at other locations. The cattails were heavily damaged by muskrats in 1978 and 1983. Arrowhead and softstem bulrush increased during the study. Fluctuations in water level may have encouraged the offshore spread of cutgrass. It grew in a line around the lake just 0.5-1.5 m from shore in water 0-0.3 m deep. Only cut-grass and infertile shoots of slender spikerush were regularly encountered with submerged plants in offshore sampling plots. They had a (mean $\pm$ 1 SE) dry weight biomass of 126 $\pm$ 64 g/m^2 for June, July,

TABLE 3. *Submerged and floating macrophytes sampled in Halverson Lake from 1977 through 1983.*[a]

Class Name	Species Name	Text Name
Filamentous green algae		
Chlorophyceae	*Cladophora insignis* (C. A. Agardhi) Kuetzing	Cladophora
	Hydrodictyon reticulatum (L.) Lagerheim	Water net
	Oedogonium sp.	Oedogonium
	Spirogyra sp.	Spirogyra
Stonewarts		
Characeae	*Chara vulgaris* L.	Chara
	Nitella flexilis L.	Nitella
Vascular flowering plants		
Ceratophyllaceae	*Ceratophyllum demersum* L.	Coontail
Haloragidaceae	*Myriophyllum exalbescens* Fernald	Northern water milfoil
Hydrocharitaceae	*Elodea canadensis* Michaux	American elodea
	Vallisneria americana Michaux	Wild celery
Lemnaceae	*Lemna minor* L.	Lesser duckweed
Najaceae	*Najas flexilis* (Willd.) Rostock & Schmidt	Bushy pondweed
	Potamogeton berchtoldii Fieber[b]	Berchtold's pondweed[c]
	P. crispus L.	Curly-leaf pondweed
	P. foliosus Rafinesque	Leafy pondweed[c]
	P. pectinatus L.	Sago pondweed[c]
	Zannichellia palustris L.	Horned pondweed[c]
Polygonaceae	*Polygonum amphibium* L.	Water smartweed
Pontederiaceae	*Heteranthera dubia* (Jacquin) MacMillin	Water stargrass

[a] Nomenclature and identifications followed Prescott (1962) and Wood (1967) for the filamentous algae and stoneworts, Voss (1972) for the Najaceae, and Fassett (1966) and Winterringer and Lopinot (1966) for the other vascular plants.

[b] Small pondweed (*Potamogeton pusillus* L.) was abundant in the lake, but synonymized with *P. berchtoldii* Fieber, following Voss (1972).

[c] Often referred to collectively as narrow-leaved pondweeds.

and August 1978.

Cattails, cut-grass, and softstem bulrush were effective in breaking wave action, trapping particulates in runoff, partly shading and cooling the water beneath them in summer, and creating quiet pockets where lesser duckweed, filamentous algae, and some detached vascular plants accumulated. The community of emergent macrophytes, although not extensive, remained an important boundary between the land and the lake.

Growth and Succession

Macrophytes with long lax stems and narrow flexible foliage dominated the submerged plant community. Curly-leaf pondweed had the widest leaves (5-12 mm). Wild celery and slender spikerush remained unbranched and offered the smallest surface area relative to biomass. Other vascular plants branched freely and produced a finely dissected foliage. A subcommunity (**association**) of "narrow-leaved pondweeds", with leaves less than 3 mm wide, dominated until mid-1982. It mostly comprised Berchtold's and sago pondweeds, but usually included some leafy pondweed and horned pondweed. These four pondweeds grew so intermingled that it was not always practical to sort them to species for separate biomass determinations. Other fine-leaved species were often found with these pondweeds, such as coontail, water milfoil, and elodea. They differed in growth form and sometimes dominated certain areas of the lake. They rarely grew alone, as sometimes reported (Verhoeven et al. 1982). Curly-leaf pondweed and water stargrass at times did form monospecific stands. The macrophyte community of Halverson Lake, consequently, comprised a dynamic array of subcommunities, differing in species composition and offering a profuse foliage of relatively large surface area.

Filamentous green algae were among the first macrophytes to appear in spring (Fig. 5). Clear water (Secchi disk greater than 3.5 m) after ice-out favored bottom growth of cladophora in deep water and spirogyra along shore. Oxygen bubbles, accumulating in mats of spirogyra on sunny days in April, forced the algae to the water surface. The mats thickened and spread as floating canopies during May and June, while bottom growth subsided. By shifting to a mud-dwelling (**epipelic**) growth, spirogyra avoided shade from vascular plants and phytoplankton blooms. The floating mats yellowed in July, but persisted longer in the cooler unharvested bay (Transect 1). Shading from blue-green algae in August (Secchi disk less than 1 m) contributed to the demise of cladophora in deep water.

Although contributing less than 5% of total plant biomass in June, floating mats of spirogyra were important as cover and habitat before vascular

TABLE 4. *Emergent vascular plants, with submerged roots and crowns, observed at the water's edge in Halverson Lake from 1977 through 1983.*[a]

Class Name	Species Name	Text Name
Alismaceae	*Sagittaria latifolia* Willd.	Arrowhead
Cyperaceae	*Carex aquatilis* Wahl.	Water sedge
	Eleocharis acicularis Rostock & Schmidt	Slender spikerush
	Scirpus validus Vahl.	Softstem bulrush
Gramineae	*Leersia oryzoides* (L.) Swartz	Cut-grass
	Phalaris arundinacea L.	Reed canary grass
Juncaceae	*Juncus* sp.	Rush
Sparganiaceae	*Sparganium eurycarpum* Engelmann	Bur-reed
Typhaceae	*Typha latifolia* L.	Cattail

[a] Nomenclature and identification mostly followed Fassett (1966) and Britton and Brown (1970).

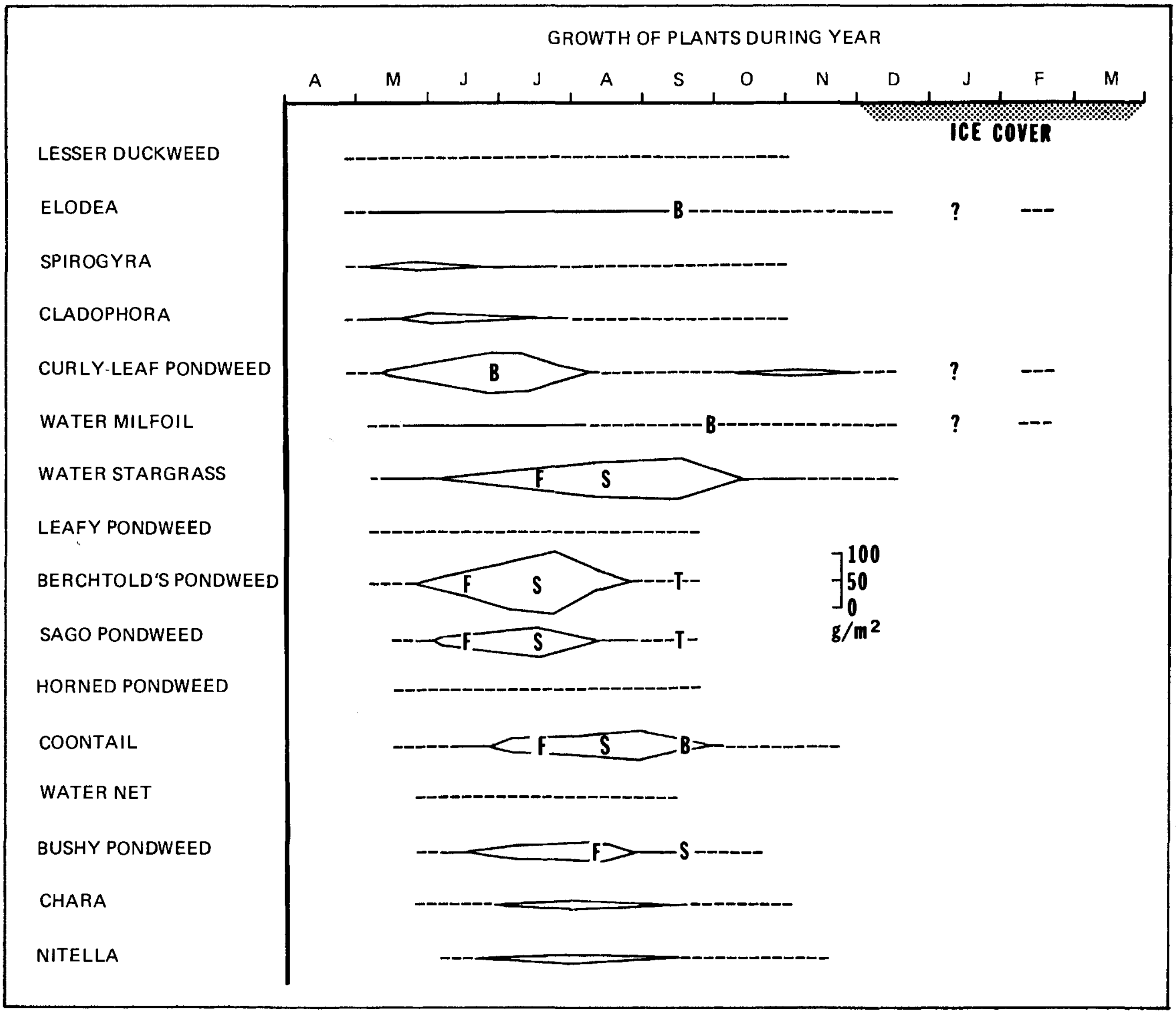

FIGURE 5. *Growth and succession of submerged and floating macrophytes in Halverson Lake (excluding Transect 1). Data are compiled for 1978, 1979, and 1982, when the lake was unharvested. Apical buds (B), flowers (F), seeds (S), and tubers (T) are noted when they first appeared.*

plants became dense. The mats trapped detritus, contributed dissolved oxygen to the water column, and attracted a variety of aquatic insects that appeared to use the mats as feeding stations in spring. Bass would occasionally hover under algal mats during the day.

Elodea and curly-leaf pondweed also appeared green at ice-out, but did not become dense until late May. Water milfoil, narrow-leaved pondweeds, and coontail followed in early to mid-May. These species occur earlier in some temperate lakes (Kollman and Wali 1976, Dale and Gillespie 1977, Macan 1977). Bushy pondweed and water stargrass appeared green in mid- to late May and only became dense after June. Nitella was finally noticed in June.

Macrophyte growth and succession in Halverson Lake was complex, because of species differences in onset of growth, growth rate, distribution, and tolerance to high temperature and low light penetration in summer.

Spring growth differed among years for some species. Curly-leaf pondweed grew before ice-out and produced its largest standing crop in 1981, when little snow covered the ice after January and ice-out occurred 19 days earlier than the 6-year median of April 2 (Table 5). Bushy pondweed, coontail, and water stargrass were denser after 1980, while nitella and cladophora were sparser. Plant harvesting and spring differences in water clarity, nutrient runoff, cloud cover, and water temperature may have varied macrophyte growth among years.

Most submerged macrophytes reached maximum biomass in July. Total production in preharvest years (1978 and 1979) increased 2-3 times from June to July for all species and reached 3,300 to 4,900 kg dry weight (Table 6). Total cover also increased during the period. Total production was not significantly different among years for July, despite plant harvesting in 1980 and 1981.

Narrow-leaved pondweeds turned yellow in August and died back to black runners on the lake bed. Shallow-water temperatures were then above 25 C. Curly-leaf pondweed yellowed several weeks earlier in shallow water, but persisted through summer in deeper water (1.3-3.5 m), in the spring-fed unharvested bay (Transect 1), and over spring seeps on the lake bed. It

TABLE 5. *Dates of final complete ice-up and ice-out, mean ice and snow depths around Station B for February 10-21, and durations of ice cover and open water.*[a]

Year	Depth (cm) Ice	Depth (cm) Snow	Ice-Out	Open Water (Days)	Ice-Up	Ice Cover (Days)
1977	—	—	Mar 25	247	Nov 26	133
1978	35	12	Apr 7	231	Nov 23	141
1979	46	24	Apr 12	234	Dec 1	127
1980	38	5	Apr 5	236	Nov 26	109
1981	44	0	Mar 14	264	Dec 2	122
1982	43	13	Apr 2	252	Dec 9	

[a] Dates of complete ice cover and ice melt were based on frequent visits to the lake and Dodgeville, Wis. weather; only ice-out on March 25, 1977 was based completely on weather data; the lake may have partially reopened in December 1982.

TABLE 6. *Total production and areal cover of submerged macrophytes for Transects 2-15.*[a]

Sampling Date		Total Production $\pm$ 1 SE (Kg $\times$ 10^2)	Total Cover (ha)
1977	Aug 18	26 $\pm$ 3	1.8
1978	Jun 6-13	17 $\pm$ 2	2.1
	Jul 27-31	33 $\pm$ 2	2.5
	Aug 28-31	7 $\pm$ 1	1.4
1979	Jun 6-11	15 $\pm$ 1	2.2
	Jul 11-20	49 $\pm$ 15	2.5
	Aug 22	6 $\pm$ 1	1.7
1980	Jun 3-10	7 $\pm$ 1	1.4
	Jun 16-17	12 $\pm$ 1	1.6
	Jul 8-9	44 $\pm$ 6	2.5
	Jul 15-23	15 $\pm$ 2	2.1
	Aug 18-19	7 $\pm$ 1	1.4
1981	Jun 3-5	26 $\pm$ 3	2.2
	Jun 17-24	23 $\pm$ 3	2.7
	Jul 8-9	35 $\pm$ 5	2.6
	Jul 21-23	13 $\pm$ 1	2.4
	Aug 10-17	9 $\pm$ 1	1.8
1982	Jun 8-9	20 $\pm$ 2	2.7
	Jul 13-14	50 $\pm$ 3	2.9
	Aug 11-12	31 $\pm$ 3	2.8

[a] Total production was calculated by multiplying the total cover (m^2) by the mean $\pm$ 1 SE density (kg/m^2); only areas with at least 1 g/m^2 (dry weight) of plants were included in determining total cover.

often dies back in warm lake water (Bumby 1977, Nicholson 1981, Kunii 1982), but persists in cooler streams and channels (Sculthorpe 1967). Bushy pondweed, coontail, and water stargrass grew until September. Cladophora slightly recovered in deep water after August.

Summer biomass and species composition changed dramatically during the study (Fig. 6). Pondweeds dominated in the main basin until 1982. Sago and Berchtold's pondweeds together comprised over 75% of the total biomass prior to plant harvesting. Their relative frequency fell to only 17% in August 1982 (Fig. 7). Curly-leaf pondweed followed in importance. During June and July it comprised about 5-20% of the biomass prior to harvesting, but increased to 20-60% after 1979. In August, however, it typically contributed less than 4% to the total plant biomass. The seasonal demise of curly-leaf pondweed was partly countered by an increase in coontail and bushy pondweed. In the main basin coontail made up less than 20% of the total biomass in June and July, but 5-35% during August. Coontail, bushy pondweed, and especially water stargrass increased following each of the four plant harvests. Water stargrass, not found in the lake before the first harvest, contributed to 70% of the total biomass by August 1982. It then remained dominant in July-September until last studied in 1985. Water stargrass in other lakes has fluctuated widely in abundance among years (Forest 1977), increased after plant harvesting and decline of Eurasian water milfoil (Wile et al. 1979), and dominated after nutrient enrichment (Dale and Miller 1978). Although species richness and evenness increased just after each harvest, the community eventually became dominated by water stargrass at the expense of the curly-leaf pondweed and some narrow-leaved pondweeds.

The macrophyte community persisted during summer in the unharvested bay (Transect 1) (Fig. 8). Coontail, curly-leaf pondweed, and (after 1981) elodea dominated. The vegetation grew during August and declined in September. Only spirogyra yellowed and died off in July. Its floating mats absorbed radiant energy and warmed to 30-33 C on clear July days.

The unharvested bay thermally stratified during summer, due to cool spring water on the bottom and absorption of solar radiation by vegetation on the water surface. The surface vegetation also blocked water movement and light penetration. The mean water temperature in July was 5-7 C lower than in shallow water of the main lake. Cooler water permitted curly-leaf pondweed to grow throughout summer. The bay, partly sheltered from prevailing winds, afforded protection for filamentous algae, lesser duckweed, unrooted coontail, and poorly rooted elodea. The center of the bay, just over 1 m deep, was not spring fed and remained poorly vegetated and turbid during summer. Total mean biomass in July was often higher than in the main basin, perhaps because of direct nutrient runoff received by the bay, which acted as a settling basin for the main lake.

Species succession and plant growth were related. Some plant species, adapted to extremes of light intensity and water temperature, partially replaced other macrophytes as they declined. Species succession was more prominent in shallow water, where more species intermixed, and proceeded gradually during summer. Changes were often more evident when viewed from a low altitude airplane than from shore. Windows developed in nearly continuous plant beds as macrophytes decayed. Die backs of curly-leaf pondweed in early July appeared from the air as "black holes" surrounded usually by sago or Berchtold's pondweeds (Fig. 9). These openings gave a mottled appearance to the plant community. They gradually coalesced into channels, creating a fenestrated morphology to the plant beds (Figs. 10 and 11). Some channels, however, were created by muskrats and rowboats. Largemouth bass, some over 400 mm long, used these channels to cruise among the macrophytes in search of prey.

Species succession remained incomplete, since the large biomass achieved in July was only partly replaced in August by spread of bushy pondweed, coontail, and water stargrass into the vacated areas. Large areas of the lake bed were not revegetated until the fol-

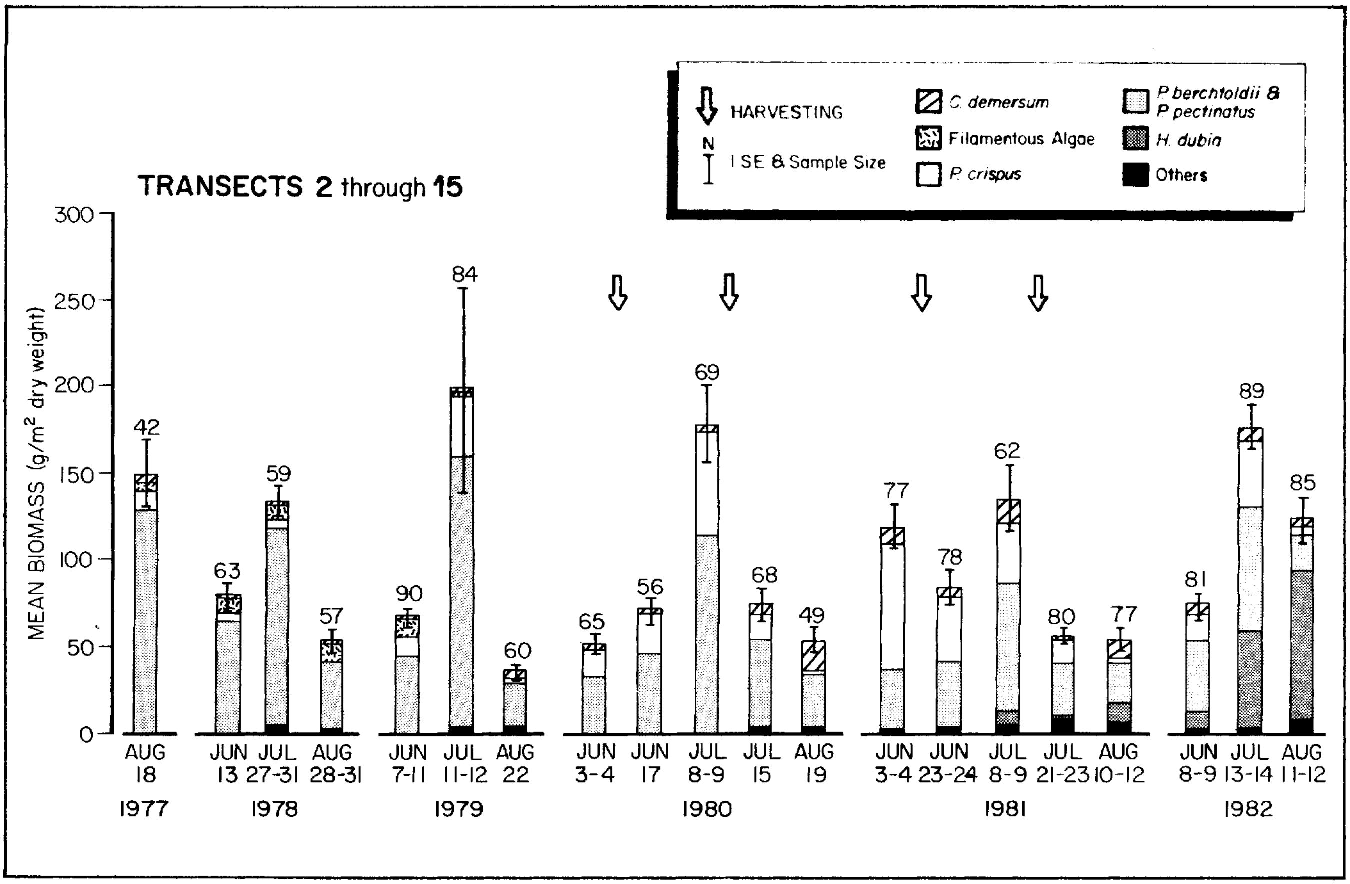

FIGURE 6. *Biomass of submerged macrophytes along Transects 2-15. Sample size on each date is shown above a standard error (SE) bar. Arrows denote the harvests.*

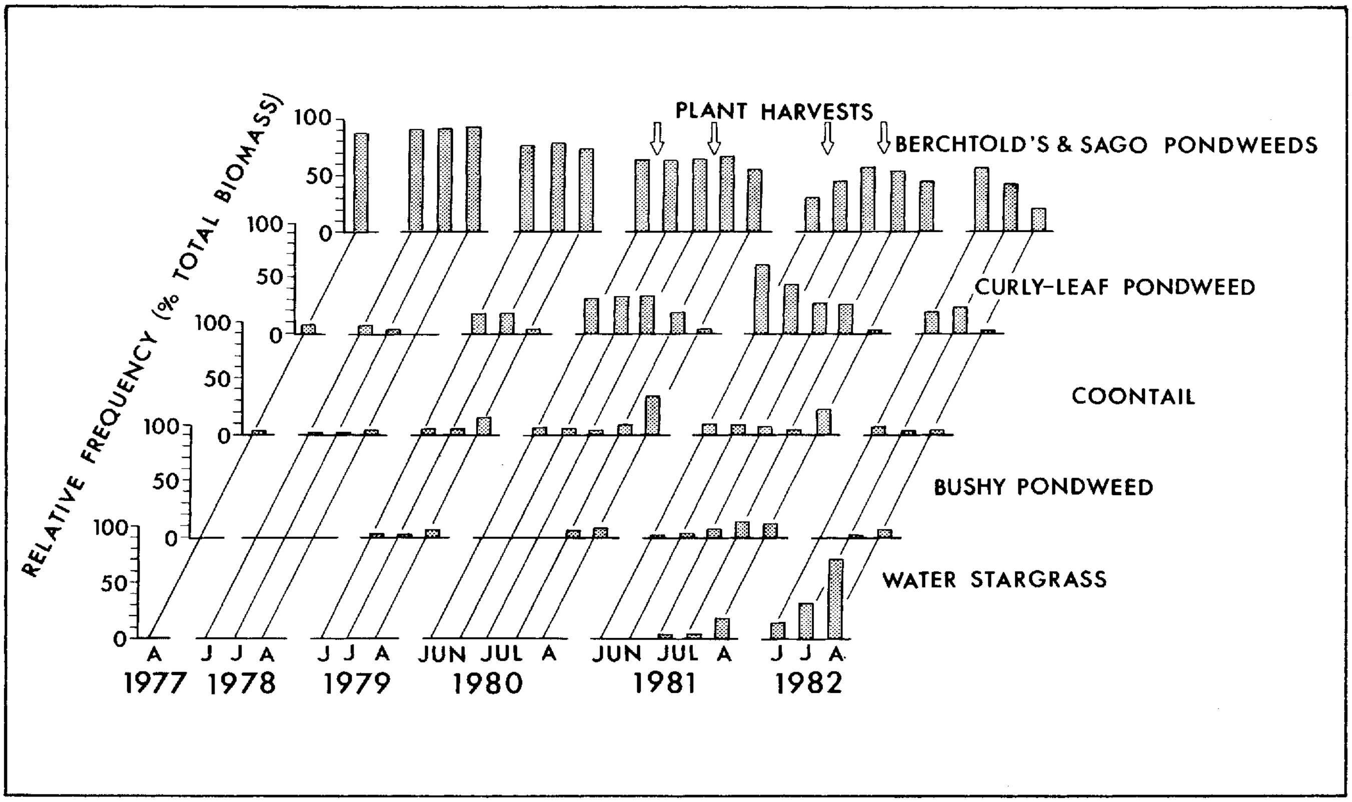

FIGURE 7. *Relative frequency of dominant submerged macrophytes along Transects 2-15.*

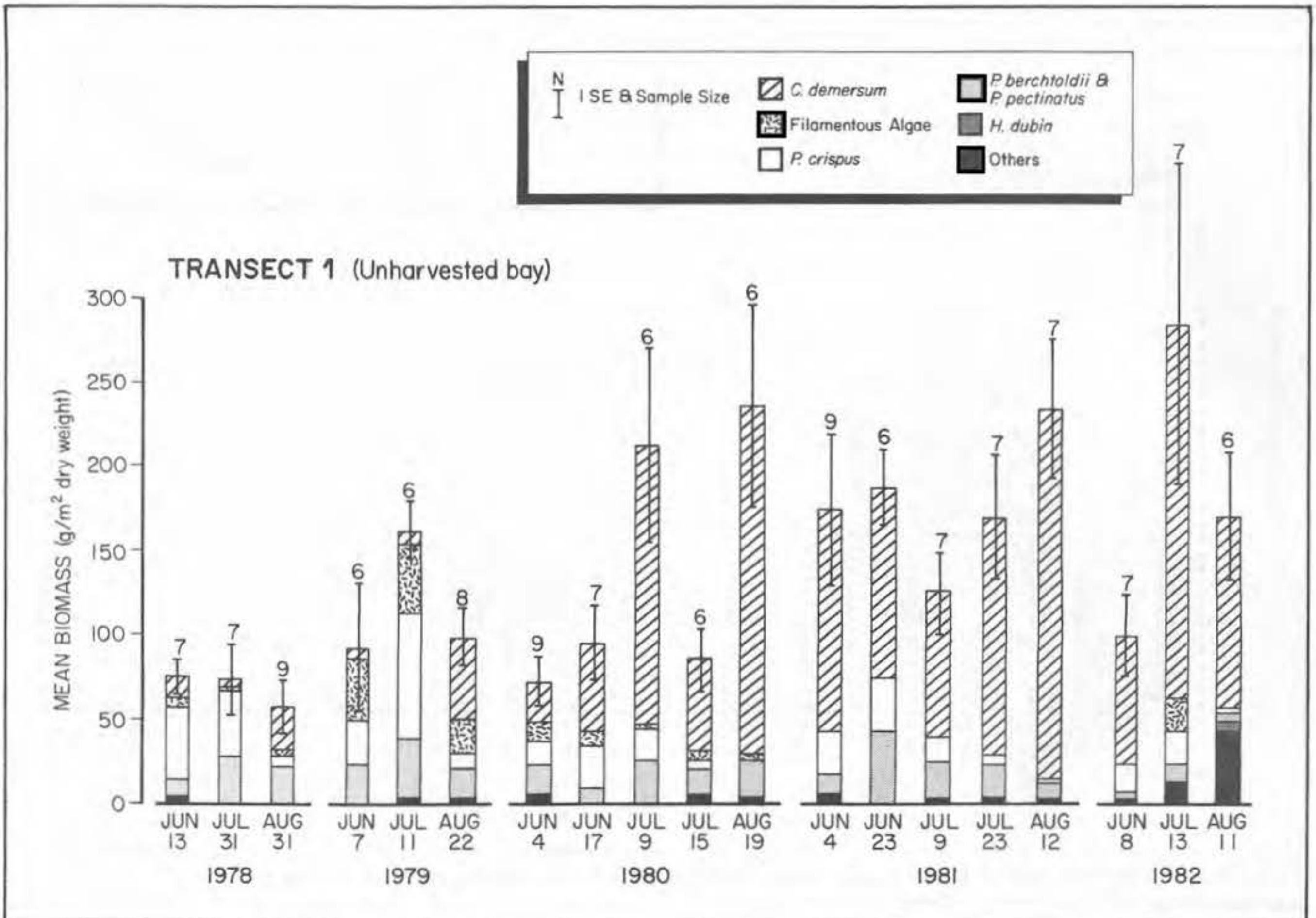

FIGURE 8. *Biomass of submerged macrophytes along Transect 1. Sample sizes and standard errors are shown above each histogram.*

FIGURE 9. *A "black hole" (arrow), formed when curly-leaf pondweed decayed, appears in a plant bed by Transect 4 on July 16, 1979.*

lowing spring. Pearsall (1920) followed a similar seasonal succession of macrophytes in the English Lake District. Macan (1977) also noted that longer-term species replacements were often incomplete, leaving bare areas on the bottom as plants disappeared.

Propagation and Winter Survival

Most submerged macrophytes relied on fragmentation and growth of runners for reproduction and dispersal during ice-free periods (Table 7). Some macrophytes were easily torn by winds, storms, and animal activity. Fishes, muskrats, and boats also spread fragments. Some were transported by incoming streams from the upland ponds. The unharvested bay was a source of fragments for the main lake, as reflected in the similarity of vegetation on either side of the dike separating the bay from the main basin (Transects 1 and 15). More fragments were produced at the end of summer and fall, when the integrity of the plant shoots deteriorated. Motor props can be especially effective in dispersing plant fragments at this time. Curly-leaf pondweed was particularly brittle throughout the growing season and more readily fragmented than most vascular plants. Fragments containing live meristem can develop into new shoots, but they are intolerant of low temperature and drying (Sculthorpe 1967).

Elodea, potamogetons, water milfoil, and water stargrass also propagated from runners. Curly-leaf pondweed produced dense (more than 600 g/m^2) mats over spring seeps that excluded other species. Some rhizomes of curly-leaf pondweed, elodea, and water stargrass survived into winter, but disintegrated on other species during fall. Filaments of cladophora turned black in fall, due to storage of organic matter (Prescott 1962), and survived winter.

Coontail, curly-leaf pondweed, elodea, and water milfoil developed winter-hardy dormant buds or **turions** on their shoots. These usually dropped to the lake bed in fall. Turions of curly-leaf pondweed developed while surface water temperature and day-length each became maximum for the year and when the plant was flowering and forming seeds. They first appeared in early June as deformed green leaves. The leaves shortened, became brittle, and turned into lateral "wings" by July. Each turion, just 2 cm long, resembled a brown pine cone. About 2-6 turions developed on a stem, with several dozen attached to each plant. Turions on other plants matured from August through October.

Turions served both for propagation and in-lake dispersal. Mature turions of curly-leaf pondweed have a specific gravity of 1.0 (Sastroutomo et al. 1979) and, therefore, float. The "wings" may serve as hydrofoils. Such turions littered all areas in August. Those of coontail, elodea, and water milfoil remained attached to the plant much longer and were not as widely dispersed. Turions of northern water milfoil often remain attached to the shoot during winter (Weber 1972, Aiken and Walz 1979).

Turions of curly-leaf pondweed form green shoots in winter (Sastroutomo et al. 1979). This could give curly-leaf pondweed a competitive edge over species with late-maturing turions or those relying on seed germination.

The other potamogetons produced less conspicuous turions and tubers on rhizomes. Yeo (1966) found tubers to be especially important for winter survival of Berchtold's and sago pondweeds, but have more limited dispersal ability than turions.

Only bushy pondweed failed to produce asexual or vegetative propagules.

FIGURE 10. *The shallow north end of Halverson Lake on July 1, 1982. Criss-crossing channels are evident within the plant beds.*

FIGURE 11. *Halverson Lake on July 13, 1982. Surface vegetation appears as light areas against the dark lake water.*

TABLE 7. *Flowering and fruiting times of submerged macrophytes and types of propagules relied upon in summer and winter.*

Species	Flowers	Fruits	Propagules[a] Summer	Propagules[a] Winter
Curly-leaf pondweed	Jun	Jul	1	Turions, rhizomes, stems
Berchtold's pondweed	Jun	Jul-Aug	1	Tubers, seeds
Sago pondweed	Jun	Jul-Aug	1	Tubers, seeds
Coontail	—	—	2	Turions, stems
Elodea	—	—	1	Turions, rhizomes, stems
Bushy pondweed	Jul	Aug-Sep	3	Seeds
Northern water milfoil	Jul	Aug-Sep	1	Turions on stems
Water stargrass	Jul	Aug-Sep	1	Seeds, rhizomes, stems

[a] Summer propagules are: 1-fragments and runners, 2-rootstocks and fragments, and 3-seeds. Turions include dormant buds or apices of Sculthorpe (1967).

It remained an annual and survived each year from seeds. Failure to grow until late spring placed it at a competitive disadvantage with other species in the lake.

Few plants grew during most winters. Green shoots of curly-leaf pondweed and coontail dotted the bottom of the main basin or were frozen into the lake ice. Larger beds of curly-leaf pondweed appeared under clear ice in February and March 1981. Water stargrass appeared yellow and moribund in winter. Elodea and some water milfoil sparsely carpeted the unharvested bay in winter. Shoots of the narrow-leaved pondweeds, however, were not found until spring.

Some pondweeds can remain metabolically active even under a snow cover (Rich et al. 1971, Boylen and Shelden 1976). Beds of coontail reached 325 g/m^2 in icebound Lake Onalaska, Wisconsin (Smart 1980). Curly-leaf pondweed remained green, but failed to grow, under the ice of a Japanese lake (Kunii 1982). Winter survival of shoots, even without growing, could be adaptive for an early growth spurt in spring and avoid delays caused by seed germination or turion development.

Sexual reproduction was important to some macrophytes. Potamogetons flowered during maximum day length in June and fruited during high water temperature in July and August (Fig. 5). Bushy pondweed, coontail, water milfoil, and water stargrass flowered in July and developed seeds from August until ice-up. Berchtold's pondweed, bushy pondweed, coontail, and some curly-leaf pondweed developed underwater flowers and fruits; other macrophytes flowered above or on the water surface and were wind or water pollinated. Coontail produced inconspicuous flowers in underwater leaf axils and released a profusion of black three-spined seeds after July. Elodea and curly-leaf pondweeds, however, were rarely observed to flower and fruit.

Sexual reproduction can provide genetic recombination, dispersal, and escape from environmental stress. Seeds of sago pondweed tend to drop near the plant (Yeo 1957), but those of other pondweeds in the lake at first float and can disperse widely. Macrophyte seeds are typically capsulated in a hard endocarp and require a cold (1-3 C) dormancy before germinating (Muenscher 1936 *in* Hutchinson 1975). The gain in population, consequently, accrues only in the succeeding spring. Asexual or vegetative methods are more important for propagation and distribution within season and are often relied upon for winter survival (Haag 1983).

Cover

The macrophyte community dramatically expanded and contracted in area each year. Maximum areal cover was reached primarily in July, when 50-70% of the lake bottom supported at least 1 g/m^2 (dry weight) of vascular plants and stoneworts (Fig. 12). Growth was rapid after mid-May and in most years over 40% of the bottom was vegetated by early June. Surface vegetation also spread rapidly after late May, when the foliage first reached the water surface. Despite a die-back of curly-leaf pondweed after June, surface foliage achieved maximum cover in late July. The narrow-leaf pondweeds contributed significantly to this coverage until water stargrass dominated after 1981.

Macrophytes recovered rapidly after each June harvesting. The harvester had difficulty cutting close to the lake bed and left offshore islands of vegetation (Engel 1980, 1983). The decline in plants after the July harvests was similar to that found in earlier years. Surface vegetation, however, was lowest during the two years of harvesting. Both bottom and surface cover changed less sharply in 1982, because of the predominance of water stargrass. It had a longer growing period than the pondweeds that dominated in earlier years. It also extended slightly deeper and reached the water surface farther offshore than had other macrophytes in earlier years. This accounted for the slightly greater plant coverage in 1982.

The unharvested bay (Transect 1) remained 90% covered with submerged macrophytes from early May to mid-September, leaving only a small central area of sparse vegetation.

From June through August vascular plants formed a nearly continuous carpet to about 3.5 m deep on the lake bottom (Figs. 13-18). Macrophyte growth ended abruptly at the edge of the former stream channel near the east shore. The vegetation extended deeper and farther offshore on the west bank. Sediment from inflowing streams and particle sorting by water contributed a softer, siltier, and less sloping bottom on the west shore. A gentle slope and soft organic sediments often support greater macrophyte growth in other lakes (Pearsall 1920, Rickett 1924, Misra 1938, Bumby 1977, Forest 1977).

Mud-dwelling filamentous algae formed a discontinuous layer beyond the vascular plants and stoneworts. They grew in patches close to the sediment surface. A thick growth was found in early years (Figs. 13-15). Inadequate sampling in deep water after 1979 (Figs. 16-18), and deeper growth of vascular plants in 1982, led to lower estimates for the algae.

Much of the water surface in the littoral region became covered with foliage. Macrophytes appeared on the water surface in early June as a thin line of plants along shore. The surface vegetation then spread over deeper water in late June and early July. Maximum surface cover was attained by late July in years when the plants were not harvested (Figs. 14, 15, and 18). Although the surface vegetation appeared continuous, close inspection revealed channels and openings that broke up the plant beds. These were areas where few plants had reached the water surface. Some areas were even devoid of plants on the lake bed. Little submerged vegetation also grew in ankle-deep water immediately along shore. Here, extremes of water temperature, waves, light, and ice scouring prevented plant growth. After late July of 1977-81, plant beds broke up rapidly, leaving islands of attached plants that finally disappeared from the water surface by mid- to late August. Little plant growth appeared at the water surface until the following May.

Harvesting produced loose floating vegetation that had to be removed with pitch forks and left islands of attached plants offshore (Figs. 16 and 17). These plants grew rapidly in June and would have covered the water surface had they not been removed in July.

Sago pondweed was the only angiosperm producing significant foliage across the water surface. Its stems repeatedly divided just below the water surface and its leaves reclined on the surface. Most other species grew to the water surface and just broke the surface tension layer. Water stargrass, however, sent its shoots 1-3 cm above the water surface. This made dense beds of water stargrass appear from a distance as dry islands.

Some areas were not revegetated each year. Both surface and bottom vegetation were nearly absent in 1980 along a portion of the east shore and by the dam (Fig. 16). In other years, vegetation here was usually not as dense as in other areas and only Berchtold's and curly-leaf pondweeds grew.

Horizontal distribution varied among macrophyte species. The pondweeds were widely distributed in the littoral region. Berchtold's and sago pondweeds grew more uniformly than most other species and occurred in over 80% of biomass samples on most sampling dates (Table 8). Their frequency of occurrence in biomass samples together dropped to 60-79% in June-August 1981 and August 1982, due to the spread of other species after harvest-

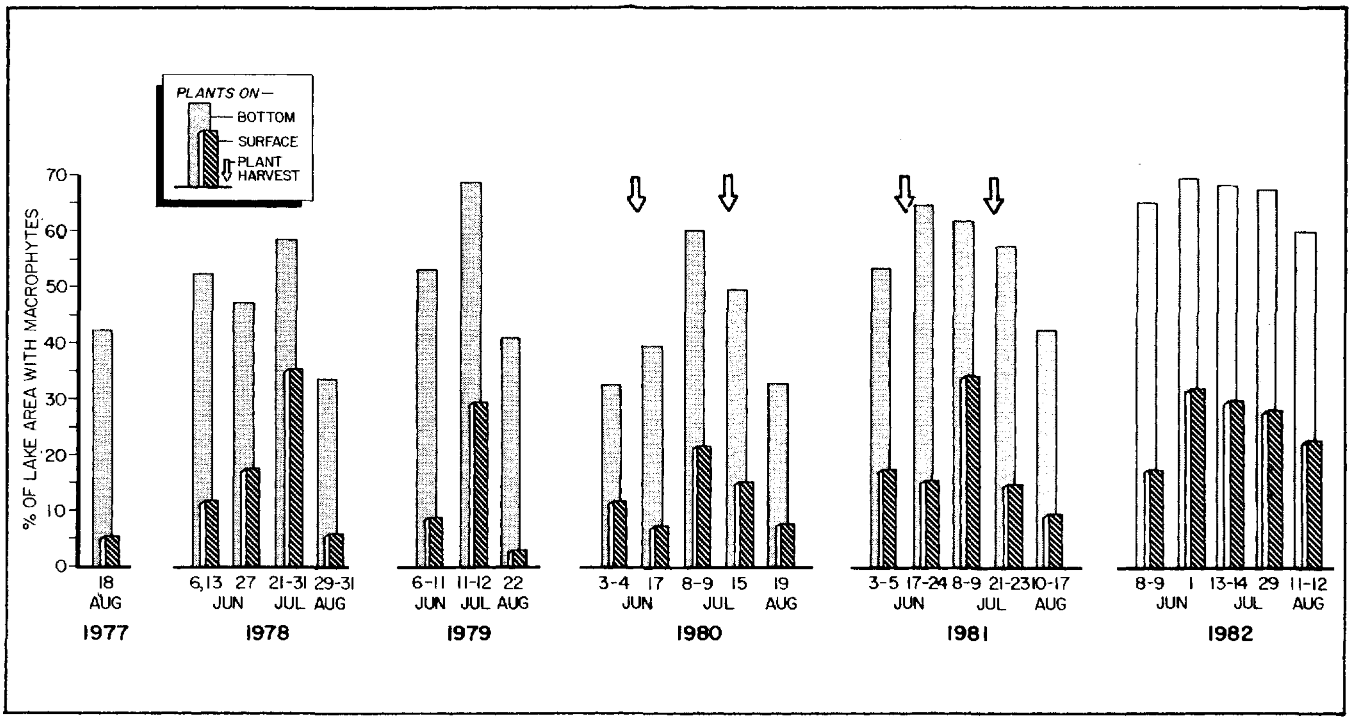

FIGURE 12. *Macrophyte cover on the water surface and lake bottom. Arrows depict the harvests.*

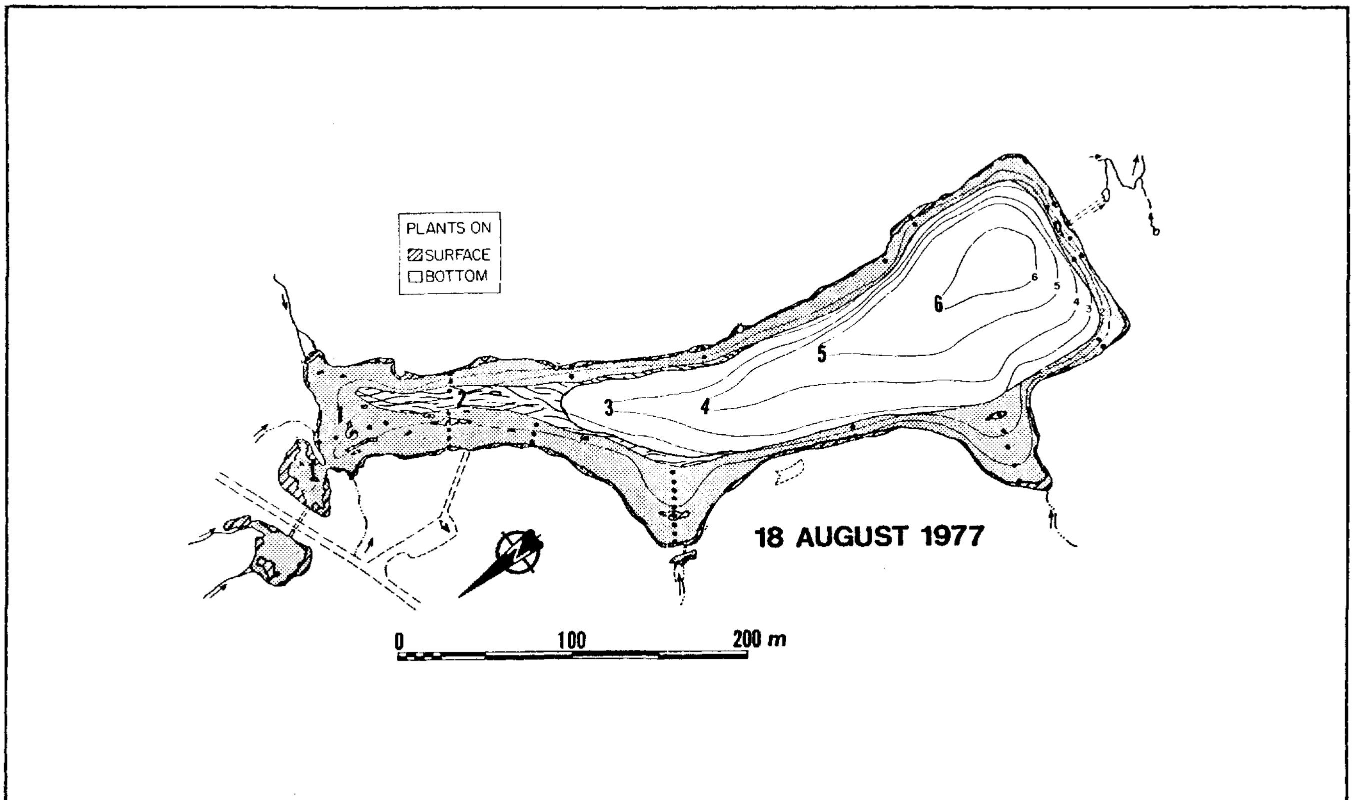

FIGURE 13. *Macrophyte distribution on the lake surface and bottom in August 1977.*

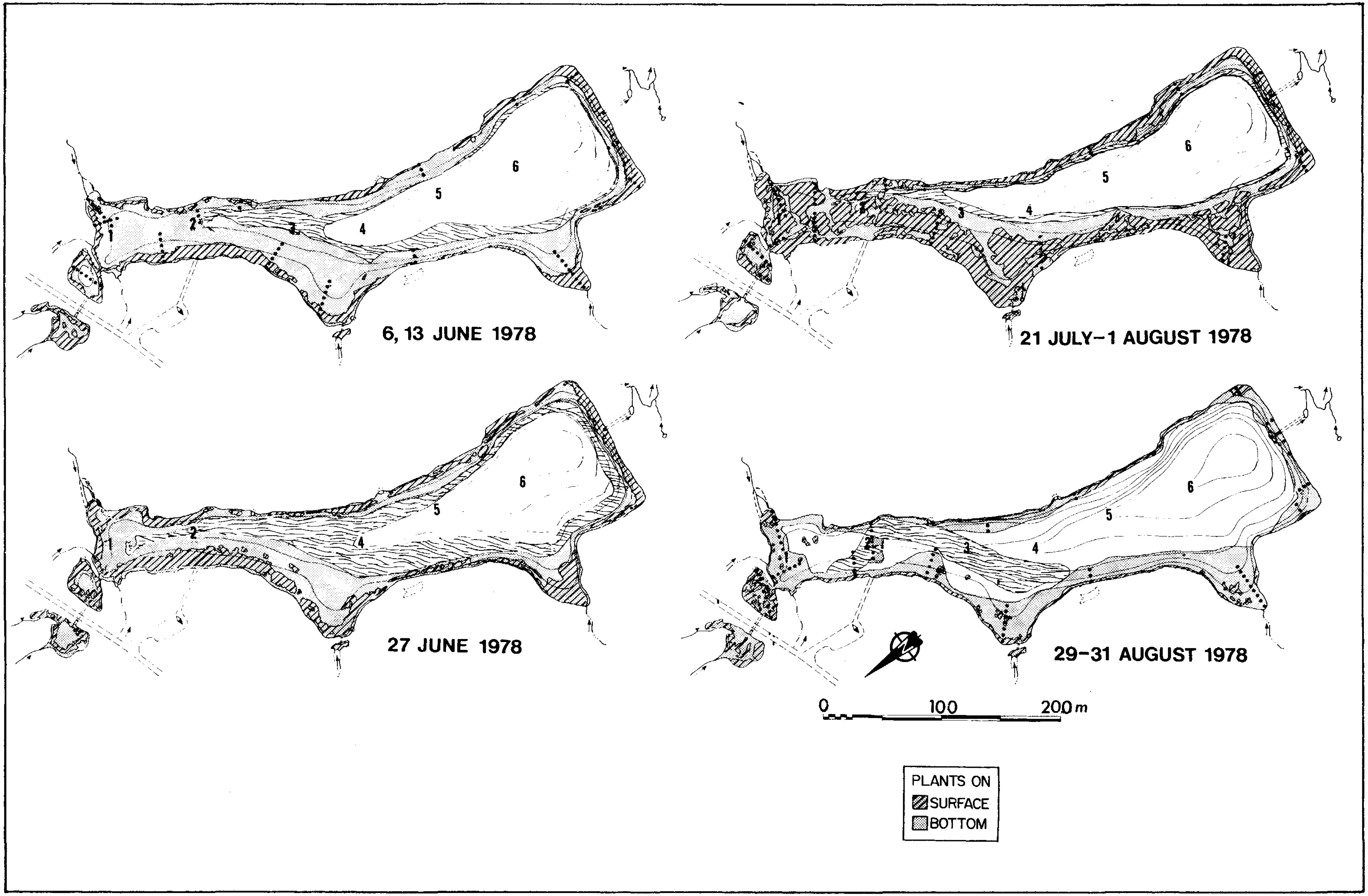

FIGURE 14. *Macrophyte distribution in June-August 1978.*

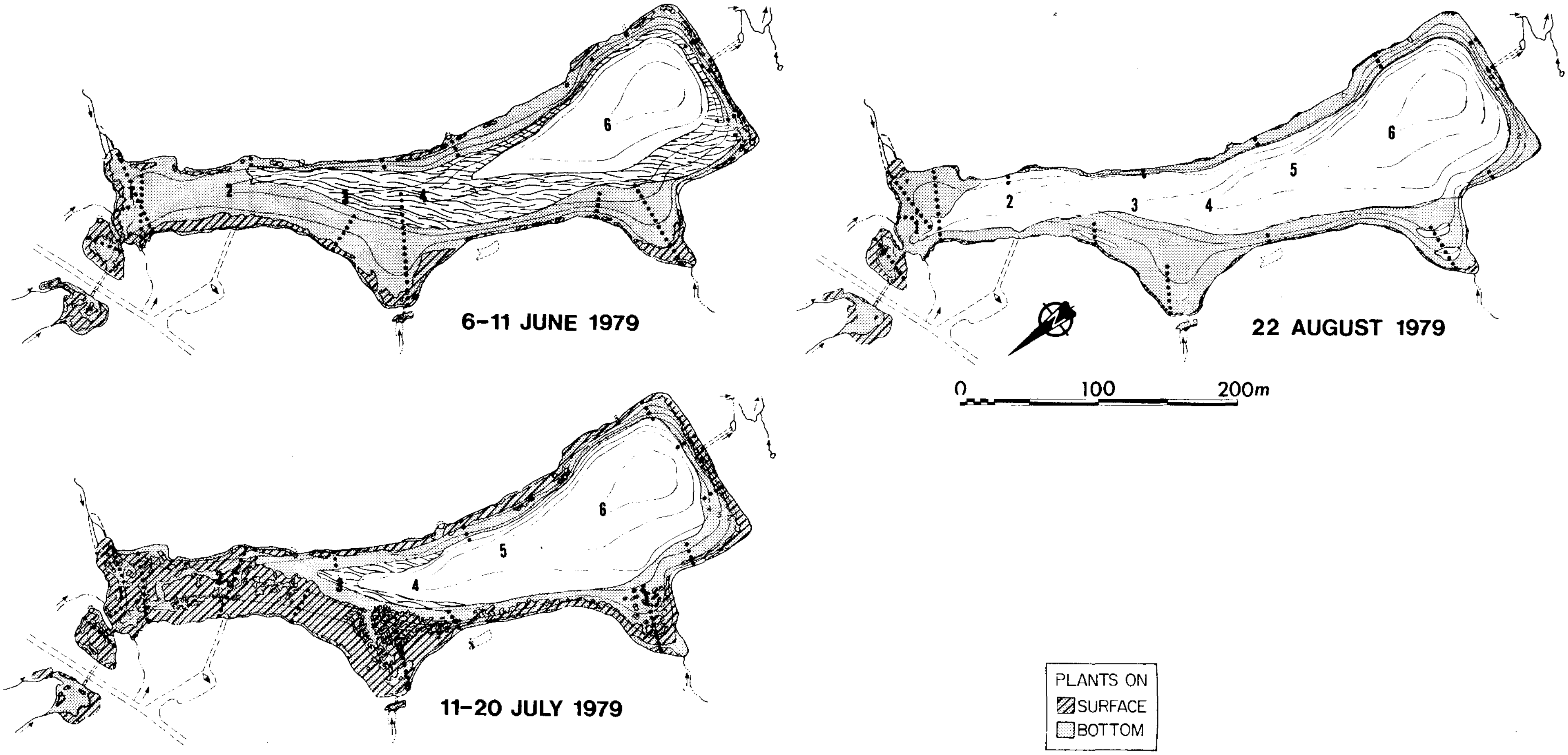

FIGURE 15. *Macrophyte distribution in June-August 1979.*

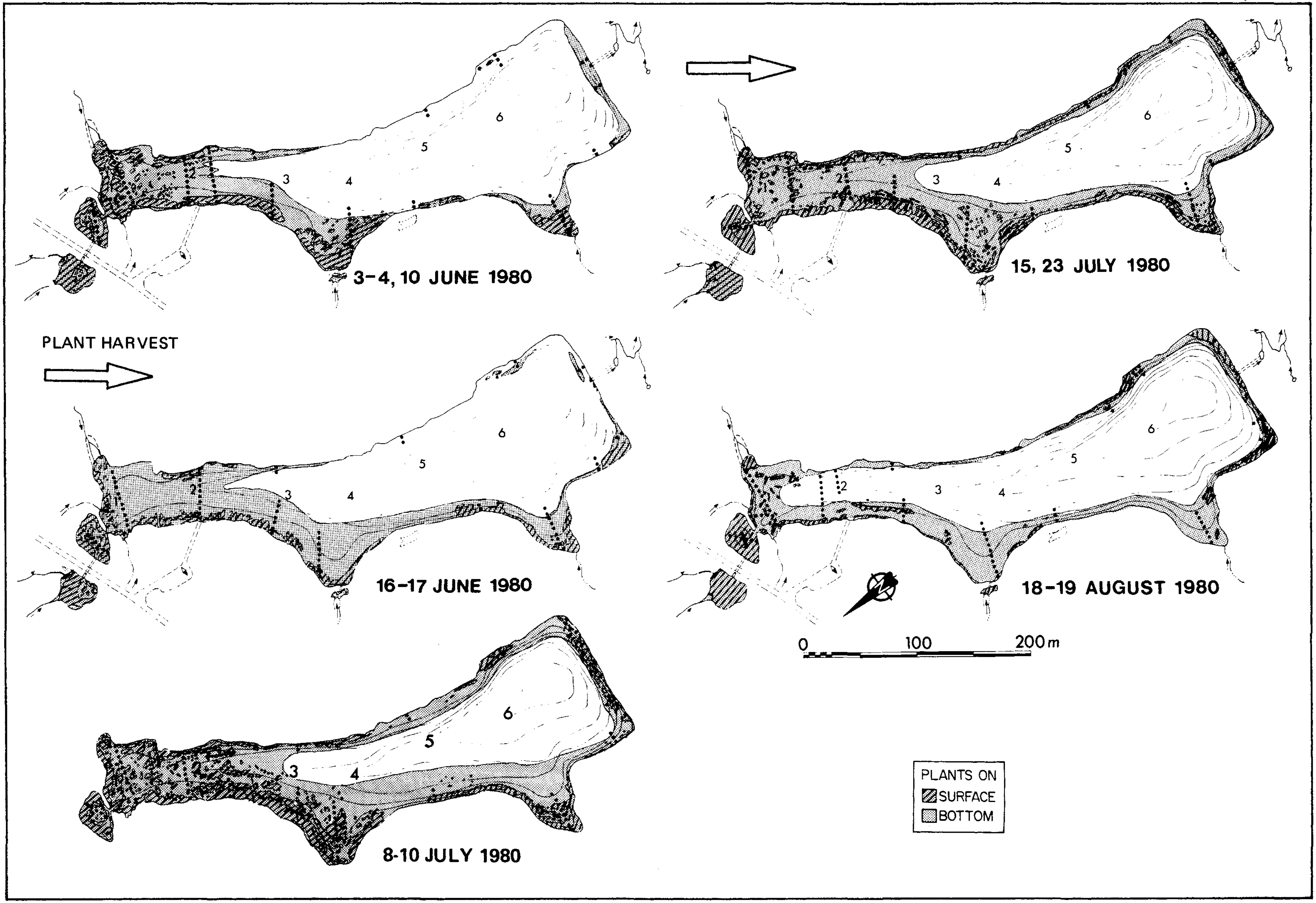

FIGURE 16. *Macrophyte distribution in June-August 1980. Arrows denote harvests.*

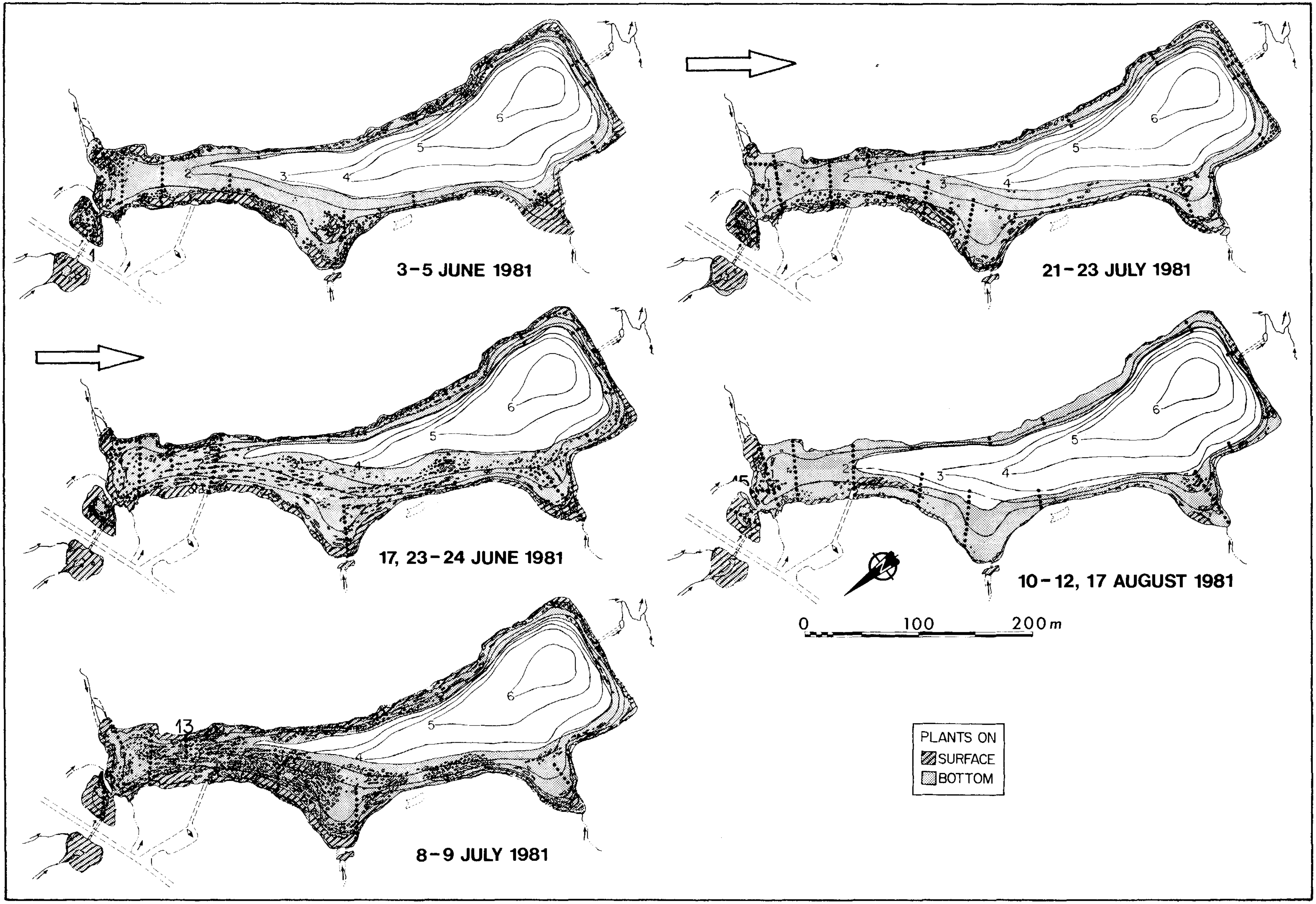

FIGURE 17. *Macrophyte distribution in June-August 1981.*

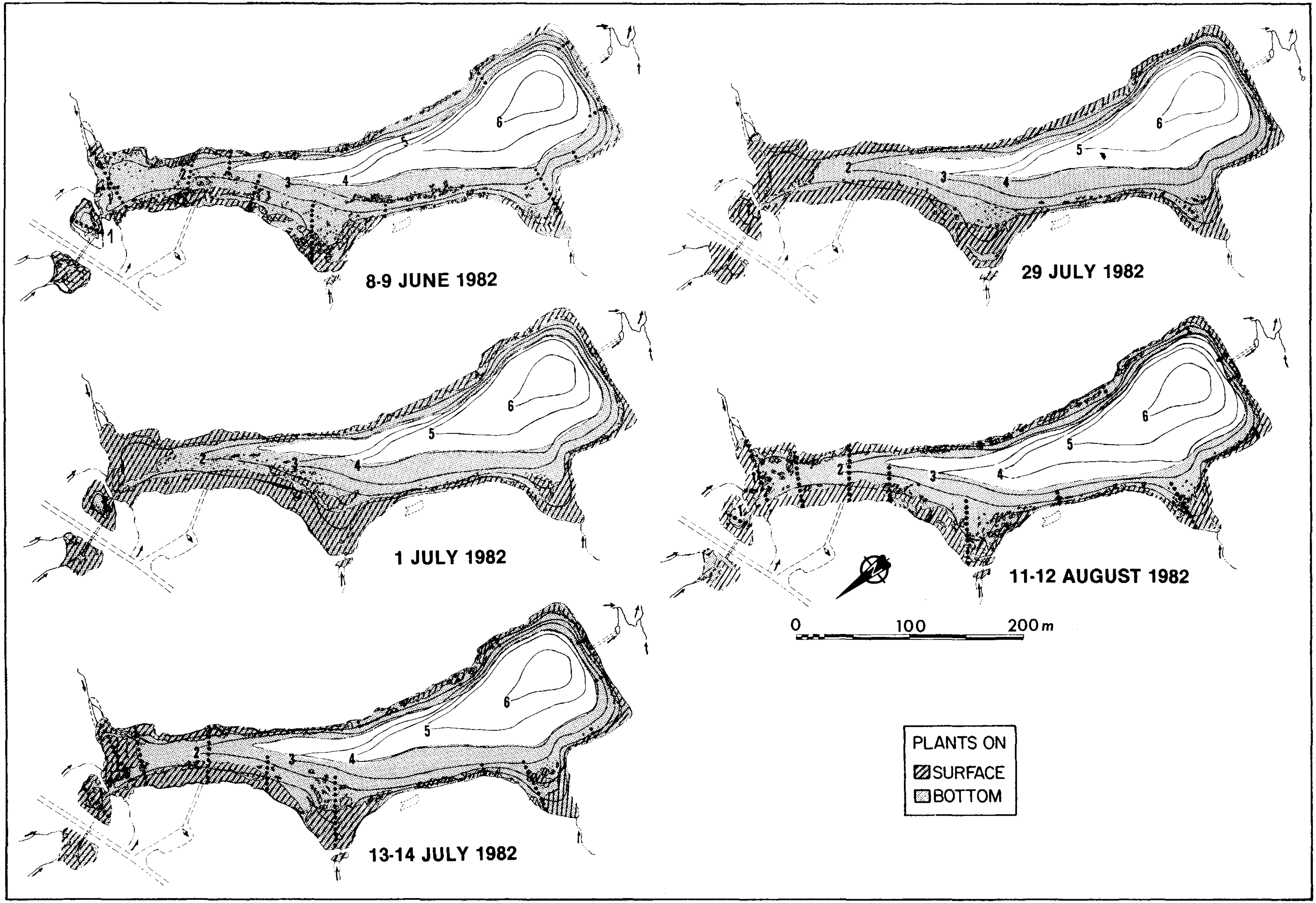

FIGURE 18. *Macrophyte distribution in June-August 1982.*

TABLE 8. *Percent frequency of submerged macrophytes at Transects 2-15.*[a]

Sampling Date		Berchtold/ Sago Pondweed	Curly-leaf Pondweed	Coontail	Bushy Pondweed	Water Stargrass	Others[b]
1977	Aug 18	100	17	33	0	0	0
1978	Jun 7-13	92	77	11	0	0	2
	Jul 27-31	92	34	3	7	0	4
	Aug 28-31	77	4	16	0	0	3
1979	Jun 7-11	81	44	12	2	0	2
	Jul 11-12	90	58	13	6	0	1
	Aug 22	90	28	18	12	0	10
1980	Jun 3-4	92	58	25	0	0	0
	Jun 17	95	79	12	0	0	0
	Jul 8-9	96	72	19	0	0	1
	Jul 15	88	68	21	19	0	3
	Aug 19	82	29	37	2	0	2
1981	Jun 3-4	77	79	31	6	3	0
	Jun 23-24	64	79	31	15	3	4
	Jul 8-9	73	71	10	24	6	2
	Jul 21-23	79	74	19	36	19	1
	Aug 10-12	73	48	30	22	31	1
1982	Jun 8-9	83	84	21	5	60	1
	Jul 13-14	89	72	21	13	88	3
	Aug 11-12	60	34	22	16	91	1

[a] Percent frequency was based on the percentage of samples with a dry-weight biomass of at least 1 g/m^2.
[b] Other species included mostly filamentous algae and some chara, elodea, horned pondweed, nitella, and northern water milfoil.

ing. Sago pondweed grew closer inshore than Berchtold's pondweed. Curly-leaf pondweed was widely distributed on most dates, but was more patchy than the narrow-leaved pondweeds. Its percent frequency peaked each June and dropped each August. Coontail, in contrast, spread to more sampling areas in August. Its maximum spread of 37% was reached in August 1980. It was more widely distributed during the two harvesting years. Bushy pondweed also spread in later years, along with water stargrass.

The growth of water stargrass was stupendous. It was first noticed along Transect 7 just after plant harvesting in June 1980. By the next year, however, it occurred commonly along the opposite east shore and areas of the shallow north end of the lake. In 1982, all transects and 70% of samples contained water stargrass. Being shade tolerant (Wilkinson 1963) it could grow beneath taller plants and mostly escape removal by the plant harvester. Harvesting the overlying pondweeds permitted greater light penetration and gave water stargrass a chance to reach the water surface. Harvesting may also have cut the apical meristems and upper shoots of water stargrass and distributed them about the lake.

Other macrophyte species were even more restricted in distribution. They usually occurred in less than 1% of samples. Chara occurred primarily along Transect 9 and occasionally by Transect 15. It grew only near shore, in contrast to its deep water growth in other lakes (Pearsall 1920, Bumby 1977). As in other lakes (Spence 1982), nitella was restricted to deep water. It grew well offshore and only along Transects 7 and 8. Water milfoil was restricted to shallow water in Transects 1, 15, and occasionally 8. It slightly increased in abundance after harvesting. Elodea was mostly found in Transect 1 and less commonly in Transects 2 and 15. It spread in 1982 and 1983 to other areas of the main lake, but only reached significant biomass in Transect 1.

Biomass samples from areas of dense growth often contained the largest number of species. Most samples from the north and west shores (Transects 2, 3, 4, 6, 14, and 15) contained 2-4 species, whereas those along the east shore (Transects 11 and 12) had only 1-3 species. Sampling diversity increased to 4-5 species in dense beds in 1982, with the spread of bushy pondweed and water stargrass. Stands of submerged macrophytes often contain few species in lakes (Swindale and Curtis 1957), because many of the less common species are patchy or restricted to a few areas of a lake. Curly-leaf pondweed, water stargrass, and chara, for example, sometimes formed monotypic stands. Although the littoral zone of Halverson Lake superficially appeared as a continuous mass of vegetation, it was in reality a mosaic of 19 submerged and floating macrophytes.

Zonation and Depth

Aquatic macrophytes partially segregated by water depth (Fig. 19). Some attached plants ranged widely offshore. Berchtold's pondweed, bushy pondweed, curly-leaf pondweed, leafy pondweed, and water stargrass grew to about 3.5-4.0 m. Growth deteriorated beyond 3.0 m, leaving short patches of plants. From mid-May to early July, when most plant growth occurred, the Secchi disk was usually visible beyond 3.5 m. Deep-water plants, therefore, were still within the photic zone. Blue-green algal blooms, thereafter, reduced light penetration and limited further growth in deep water.

Lesser duckweed and filamentous algae were not restricted by water depth, as they freely floated on the water surface. Coontail occasionally became detached and floated. These plants, nonetheless, grew in specific areas of the lake, partly due to water movements.

Many species of macrophytes grew within narrow depth limits, forming marginal, shallow-water and deep-water zones (Fig. 19). The zones were difficult to precisely delimit, because of overlap among species, their disjunct distributions, and seasonal or yearly changes in growth.

The marginal or shore zone usually extended 1-2 m offshore in water 0-0.3 m deep. Bulrush, cattail, cut-grass, and slender spikerush predominated. Their crowns and roots were submerged, but their shoots extended above high water level (eulittoral zone). Wave activity, ice-scouring in late winter, and very high water temperatures (above 30 C) in July and August restricted colonization of the marginal zone. Lesser duckweed and water net frequently accumulated in lee pockets among the emergent plants. Few submerged plants, however, grew in

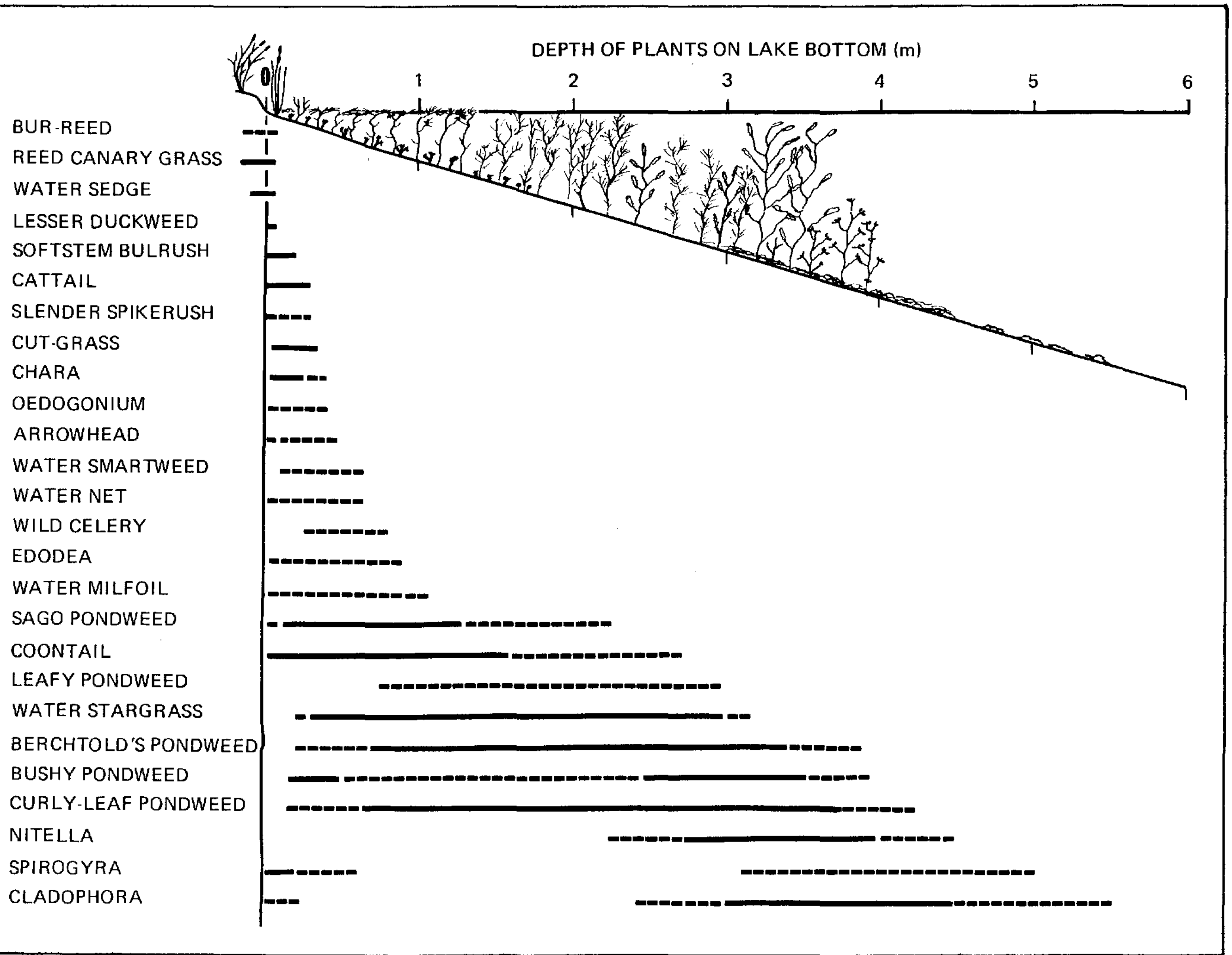

FIGURE 19. *Depth range of macrophytes on the lake bottom along Transects 2-15. Dashed lines indicate sporadic or sparse plant cover (less than 1 g/m² dry-weight biomass).*

the zone. Infrared aerial photographs revealed the zone as a clear, nearly plant-free line along the west and north shores (Fig. 11). Marginal vegetation was scarce along the steep east shore, partly due to shade from trees on the bank.

The shallow-water zone extended from a water depth of 0.3 m to about 3.5 m. It covered the largest area in the littoral region. The zone was mostly beyond reach of bottom disturbances from waves and ice movements. Particulates entering the lake in runoff principally sedimented and the lake bed was further enriched by plant remains. The zone could be divided into an inshore and an offshore region.

The inshore region of the shallow-water zone extended to a depth of 1.3 m. Macrophytes grew to the water surface. Sago pondweed predominated, but chara, cut-grass, elodea, and water milfoil occurred. Floating mats of spirogyra and some cladophora accumulated in this region. The largest species diversity in the lake occurred in the inshore region. Channels and windows were best delineated among the dense macrophytes. The region often had the largest sample biomasses (Fig. 20).

At the outer edge of the littoral region, beyond reach of surface vegetation, the offshore region bordered open water. Water stargrass and Berchtold's, bushy, and curly-leaf pondweeds variously predominated to a depth of 3.5 m. Both regions of the shallow-water zone contributed over 90% of the bottom cover and total biomass of submerged macrophytes in the lake.

The deep-water zone extended as a narrow carpet of sparse vegetation beyond the shallow-water zone. Nitella thrived only in this zone, growing from 2.5 m to 4 m, along Transects 7 and 8. Cladophora and some spirogyra formed at the base of nitella, but mostly grew where other macrophytes were sparse or absent. These plants formed a **littori-profundal zone** (Wetzel 1983) between oxygenated and seasonally anoxic sediments. The vegetation grew within the metalimnion and lower epilimnion in summer. They sprouted later in spring than inshore plants. The growing season of deep-water plants was further shortened by shade from phytoplankton blooms after mid-July. Algal blooms or other turbidity frequently limit the depth of macrophytes in Wisconsin lakes (Rickett 1924, Wilson 1941, Belonger 1969, Richardson 1974).

Total macrophyte biomass declined with water depth. Greatest biomass occurred from depths of 0.2 m to 1 m (Fig. 21). The entire water column was foliated to a depth of about 1.3 m, the limit of surface vegetation offshore. Plant height then rapidly decreased with depth, leaving a progressively shorter column of vegetation. Correcting for plant height (g/m^2 divided by water depth = g/m^3) still produced a declining curve of biomass against water depth. Plant density (g/m^2) was greatest at a depth of 1 m, but standing crop (g/m^3) was maximum at 0.2-0.3 m.

Vegetation zones are common in lakes (Curtis 1959, Spence 1982). The marginal zone of Halverson Lake is approximated by the "reed-swamp" zone of European lakes (Pearsall 1920, Schiemer 1979, Spence 1982). Hard wa-

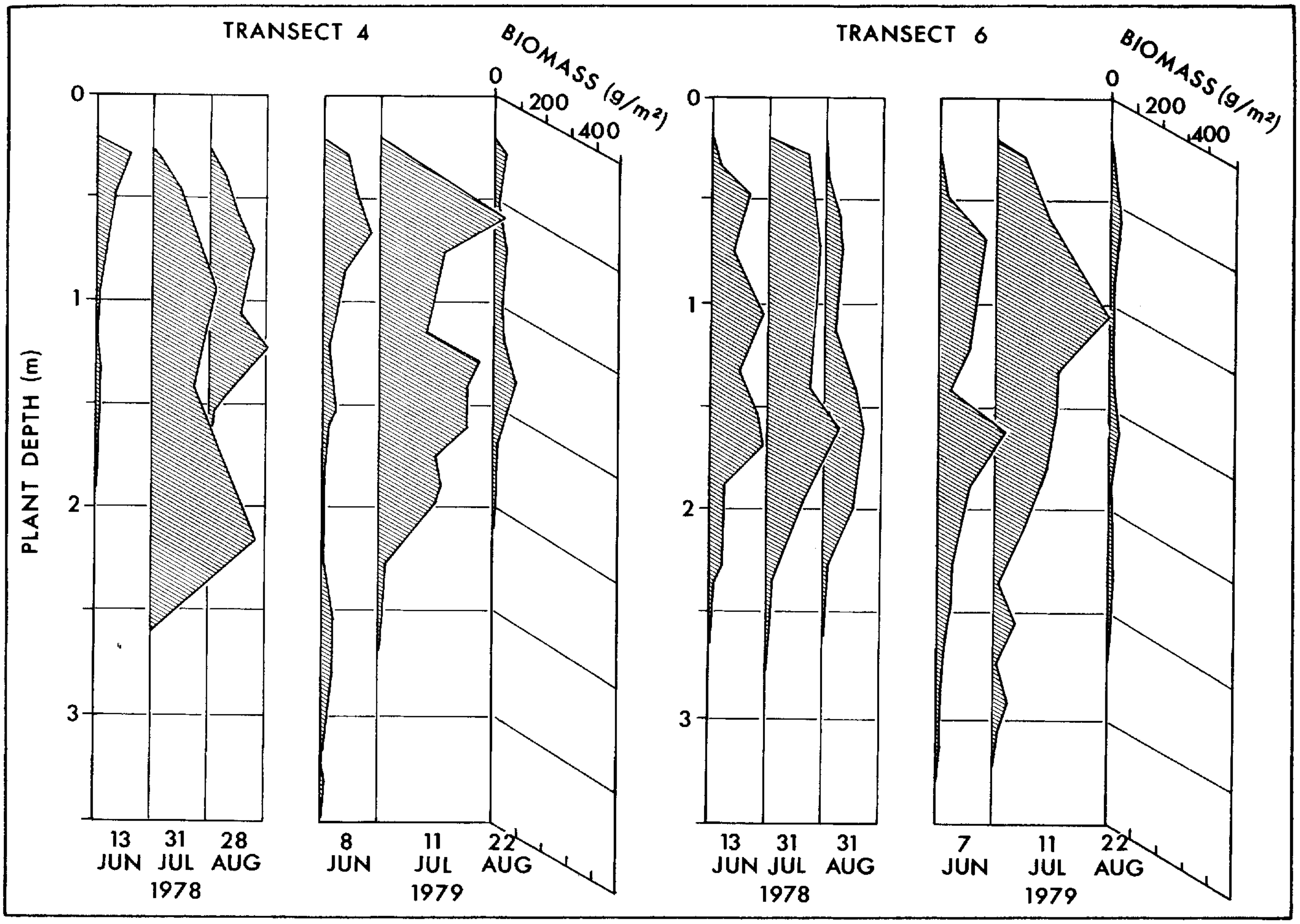

FIGURE 20. *Depth distribution of macrophyte biomass (dry weight) along Transects 4 and 6 in 1978 and 1979.*

ter lakes of Wisconsin frequently contain cattails and bulrushes rather than reeds (*Phragmites australis* (Cav.) Steudel). These species typically cannot withstand prolonged submersion of their roots and crowns. Lowering water levels permits some plants to colonize the marginal zone and alter species diversity (Beard 1973, Nichols 1975). Slender spikerush and cut-grass may have benefited from water level changes of about 0.3 m or greater after storms in Halverson Lake. Water levels otherwise changed little in the lake, discouraging the offshore spread of most emergent species.

Vertical Stratification

The foliage of shallow-water macrophytes was vertically stratified into canopy, midwater, and basal layers.

A canopy formed on the water surface and extended 10-15 m offshore. Spirogyra dominated the canopy before June; sago pondweed was the principal plant in June and July. Lesser duckweed and aerial portions of water stargrass shoots also occurred in the canopy. Foliage of sago pondweed extended 0-60 cm below the water surface. The canopy reduced light pene-

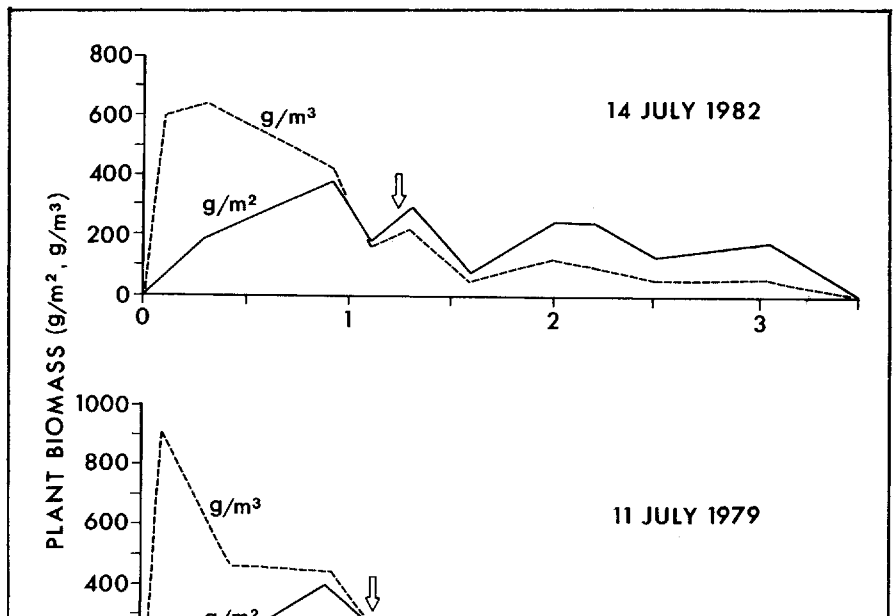

FIGURE 21. *Total macrophyte biomass (dry weight) along Transect 6 in July 1979 and 1981 compared by g/m² and g/m³. Arrows denote the offshore limit of plants on water surface.*

tration, prevented wind from stirring the water column and distributing heat, and absorbed solar radiation. The canopy contained many flowers, fruits, and algal spores. A biogenic thermal stratification developed on warm days in July. The canopy reduced plant growth under it and selected for coontail and other shade-tolerant species. Macrophyte photosynthesis can decline sharply below a canopy, because of light restriction, older plant tissues, and lower nutrient uptake in the deeper water (Adams and Prentki 1982).

A midwater layer of macrophytes grew intertwined from the lake bed to the water surface. It extended into much deeper water than the canopy layer. Berchtold's and curly-leaf pondweeds predominated during most years; water stargrass became dominant after 1981. The growth of most species was sparser offshore. Light, heat, and the force of the wind could reach the lake bottom offshore, where the canopy was sparse or absent. Water temperatures were nearly homoiothermal on windy days, but gradually diminished with depth on calm days.

A basal or crown layer of plants formed at the base of taller vegetation. The layer contained both mature and immature shoots. Coontail, bushy pondweed, and water stargrass dominated the basal layer in the main lake; coontail and elodea were most important in the unharvested bay. Coontail was noticed at the base of Eurasian water milfoil in Lake Wingra, Wisconsin (Carpenter 1980*b*). These understory plants are shade-tolerant (Wilkinson 1963, Sculthorpe 1967, Carr 1969) and, therefore, can thrive even under a dense canopy of sago pondweed and filamentous algae. They continued to grow later in the summer than the potamogetons, despite dense blooms of blue-green algae. The plants were typically less than 15 cm tall in May and June, but grew rapidly toward the water surface after die-back of pondweeds in July and August. Plant harvesting also exposed the basal plants and permitted them to grow rapidly toward the water surface. The layer was less developed in deep water, however, and was largely replaced by a bottom cover of cladophora.

Vertical stratification of submerged macrophytes in Halverson Lake recalls the vertical structure of vegetation in interior tropical rain forests (Richards 1966). Green foliage, flowers, and fruits in humid forests, as in Halverson Lake, are abundant in the upper well-lighted canopy. Sunlight is sharply extinguished, leaving a sparse bottom growth. Interspecific competition for light and space can be intense. Monotypic stands are rare. Both communities support closely allied species living together. The narrow-leaved pondweeds of related and morphologically similar species dominated Halverson Lake in most years. The lake also contained more species of macrophytes than commonly reported for eutrophic Wisconsin lakes (Belonger 1969, Modlin 1970). Few species ever became abundant. A large number of rare plant species also characterizes undisturbed rain forests (Fedorov 1966).

Plant community development can be reversible. Loss of a tree creates an opening on the rain forest floor, permits greater light penetration, and stimulates vigorous growth of both new plant species and their associated plants and animals. In a similar manner, mechanical harvesting in Halverson Lake permitted greater light penetration and stimulated growth of water stargrass. Logging and chemical defoliation in rain forests, like plant harvesting and herbiciding in lakes, can disturb long-term community stratification.

Lakes and rain forests differ. The macroscopic flora of temperate lakes are dwarf, depauperate communities compared to rain forests. The gargantuan communities of South American lowlands are dominated by woody plants towering 40-60 m high, about as tall as the bluffs surrounding Halverson Lake. The littoral forests of temperate lakes consist of delicate plants scarcely a few meters tall. Unlike the perpetual evergreen foliage of the tropics, macrophyte community development in northern lakes is annually interrupted by a long winter diapause. The short growing season in northern lakes places a premium on early growth and synchronized production of fruits to ensure cross pollination. Species succession in lake vegetation is partly an expression of the short, but rapidly changing conditions of the growing season. Rapid community turnover is rare in the tropics.

Other differences exist. Rain forests locally contain hundreds of plant species (Richards 1966); aquatic macrophyte communities rarely exceed a few dozen species. Both undisturbed communities can be vertically stratified, but the dominant aquatic plants branch repeatedly near their crowns and resemble more closely tropical shrubs than trees. Unlike tropical rain forests of long standing, aquatic macrophyte communities form part of an ephemeral stage in a hydrarch succession toward drier vegetation. Despite these many differences, mature lakes and forests offer insight on community development. Study of undisturbed vegetation provides a basis for understanding and ultimately managing more disturbed plant communities.

Vertical stratification of aquatic macrophytes may fail to develop in lakes. Low fertility and great relative depth restrict macrophyte growth in some large, deep lakes. A short growing season, hard lake bottom, low pH, and infertility suppress macrophyte growth, species composition, and community development in many lakes of the Canadian Shield (Magnin 1977). Such lakes in northern Wisconsin often support a sparse covering of short rosette plants, including quillwort (*Isoetes* spp.), infertile spikerush (*Eleocharis* spp.), and wild celery. These are replaced by bushier plants in Halverson Lake and many waters south of the Shield (Fassett 1930). Plants of the rosette type divide in or near the hydrosoil, producing a whorl of ribbon-like leaves from a common underground node. Dry weight biomass rarely exceeds 100 g/m^2. The dominant plants of more southern waters divide repeatedly above the hydrosoil, shading plants beneath them. Mean dry weight biomass can reach 600 g/m^2 in Wisconsin (Engel and Nichols 1984). The extent of vertical stratification in Wisconsin lakes, consequently, reflects both the growing conditions and the type of dominant vegetation

Submerged macrophyte beds can curtail water circulation (Madsen and Warncke 1983). Halverson Lake was partly sheltered by surrounding hills and received surface runoff less directly through ponds and fresh meadows. The several tiers of macrophytes provided a more effective barrier to water movement. In contrast, the foliage of Eurasian water milfoil in Lake Wingra, Wisconsin mostly grew near the water surface. Runoff to this lake occurred rapidly during storm events, when slightly colder incoming water sank beneath the macrophyte canopy and flowed into the pelagic region (Weiler 1978 *in* Adams and Prentki 1982). The density of the runoff water and dearth of foliage below the canopy combined for a rapid exchange of water with the pelagic region.

Vertical stratification ultimately adds a dynamic three-dimensional structure to aquatic macrophyte communities. Its maximum development is achieved in relatively undisturbed, but eutrophic littoral regions. Continual human disturbance and invasions of exotic macrophyte species can simplify vertical development in lakes. The importance of vertical stratification in macrophyte communities, consequently, has often gone unrecognized.

Microclimates

The sparse cover of submerged macrophytes in the marginal zone was produced by wave and ice movements, high water temperature, sedimentation, and shading.

Wave and ice movements were major factors hindering plant colonization inshore. Mechanical scouring of the lake bed inshore by waves and ice destroyed young shoots and removed plant propagules. The ice often appeared brown inshore as surficial deposits became frozen into the ice. Some plant shoots also became trapped in the ice and were torn loose during ice-out. Maximum ice thickness was about 0.4 m on Halverson Lake (Table 5). This approximated the maximum depth of the marginal zone. Waves were important especially in spring and fall, because of the prevalence of storms at these times, absence of thermal density gradients in the water column, and scarcity of offshore macrophyte beds to intercept the water and soil movements. Prevailing winds in spring and fall were typically from southeast-southwest, directing the greatest mechanical energy against the north and west shores of the lake. The breaking waves eroded the shoreline in places and carried away sediments.

High water temperature in the ankle-deep water along shore may also have suppressed plant growth and development. Water temperatures here reached over 40 C on some July and August days and then dropped at night. These conditions may have taxed the adaptability of many plants and ectothermal animals.

Some areas along shore were occasionally smothered in sediment. The one or two samples collected in the shallowest water along Transect 14 were often devoid of plants, due to heavy sedimentation from one of the permanent streams just after a storm. Coontail repeatedly attempted to colonize this site without success. Macrophytes were also destroyed by wind erosion of a sand blowout on a steep bank by Transect 5 (dotted rectangle in Fig. 2). Siltation was heavy in 1981 and 1982 after beavers removed young willows (*Salix* sp.) in front of this bank. Muskrat tunneling along the dam and areas of the west shore contributed to erosion and sedimentation by loosening bank soil.

Shading from high banks and trees appeared to reduce plant biomass and diversity along the dam (Transects 8 and 9) and east shore (Transects 10-13). The high bluff along the east shore cast a morning shadow evident on infrared aerial photographs (Fig. 22). This shore received several hours less direct sunlight than did the opposite shore. Vegetation was scarce under branches of red cedar trees (*Juniperus virginiana* L.) growing by the east bank. Black alder trees (*Alnus glutinosa* Gaertn.) have been planted along streams in Europe to suppress submerged macrophytes and lower water temperature for trout (Krause 1977,

FIGURE 22. *Shadows cast by trees along the east shore at 7:00 a.m. (CST) of August 1, 1978.*

Dawson 1978, Dawson and Kern-Hansen 1978). Well-shaded stream banks not only lower total biomass, but support fewer plant species (Jorga et al. 1982). Growing trees along certain lake shores could be a long-term management option for limited control of submerged macrophytes.

On warm days in July, submerged macrophytes absorbed solar radiation and heated the surrounding water through forced convection and conduction. Water temperatures were 2-3 C higher above plant beds than in nearby areas without them (Table 9). The temperature dropped 10 C from surface to bottom in vegetated areas without bottom springs, but decreased only a few degrees in unvegetated areas. Dale and Gillespie (1977) noted a similar temperature gradient through plant beds. Absorption of solar radiation by the surface foliage, with restriction of water movements, accounted for the thermal stratification.

Isotherms in Halverson Lake were lower on the lake edge of macrophyte beds and bent under or between foliage toward shore (Fig. 23). Such bending of isotherms was most pronounced in shallow water, where plant beds were denser. Heat was liberated to the atmosphere at night, but the surface water above the macrophytes remained warmer than that in open water. Extreme water temperatures (40 C) were reached in the marginal zone during the day, due to absorption of solar radiation by the dark bottom. Heat loss at night lowered water temperature in the marginal zone below that over dense vegetation of the shallow-water zone.

Nutrients in Macrophytes

There was no evidence that nutrients limited macrophyte growth in Halverson Lake (Table 10). Nutrient concentrations varied among sampling dates for each species, but no seasonal or yearly trends were evident. Being water soluble and mobile across cell membranes, potassium leached from the plants during thawing and yielded low mean concentrations. Plants in 1982 were not frozen and had much higher potassium levels. Calcium concentrations were high, because of marl remaining on the plants after washing.

Mean concentrations of nitrogen and phosphorus were within the range reported for the same species in nearby Cox Hollow Lake (Richardson 1974). They were higher than Gerloff's (1973) critical growth-limiting levels of 0.1% P and 1.3% N for subterminal tips of coontail. Adding nutrients to the lake might have increased macrophyte density, but probably would not have expanded its total plant cover. An increase in benthic algae might instead have occurred from additional nutrient loading (Cattaneo and Kalff 1980) or a phytoplankton bloom might arise that could shade macrophytes and limit growth in deep water.

BOTTOM AND PLANT DWELLING FAUNA

Community Composition

Macroscopic invertebrates comprised a large and varied community in Halverson Lake. They occupied diverse habitats and comprised over 140 species. There was one-fifth and one-half more species of macroinvertebrates than species of phytoplankton and zooplankton, respectively (Table 11). More species were collected inshore on submerged macrophytes (78 species) than on the lake bottom (61) or in midwater on multiple-plate samplers (55). The littoral region was richer in bottom species than the profundal region (20). Many species, however, were rare or seldom encountered, leaving a smaller pool of recurring species. The mean Shannon-Weaver diversity indices for bottom samples, pooled for all years, was thus not significantly different from either pooled zooplankton or phytoplankton samples, based on unequal-variance *t*-tests. Because many of the insects had numerous morphologically distinct instars, the macroinvertebrate community was even richer than would be suggested from the number of species.

Aquatic insects comprised about three-fourths of all macroinvertebrate species (Table 12). They were classified into 45 families and 9 orders. Usually only 1 species was identified for each

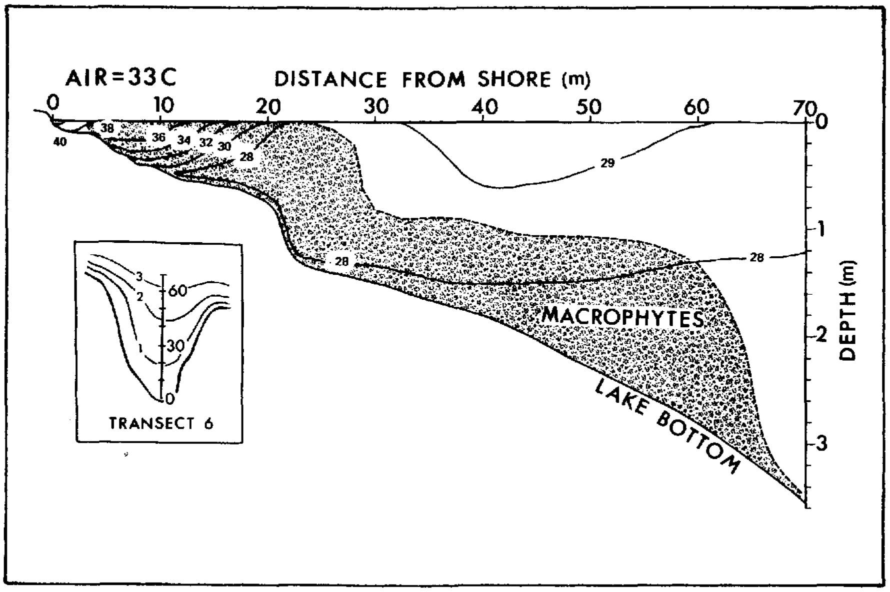

FIGURE 23. *Isotherms (C) through macrophyte beds along Transect 6 around noon on a warm sunny day (July 14, 1983). Inset shows aerial sketch of the lake at Transect 6.*

TABLE 9. *Water temperatures (C) through and just outside macrophyte beds in a sheltered (Transect 1) and unsheltered (Transect 3) bay on July 14, 1983.*[a]

Transect	Plants	Depth (m) 0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	Mean ± 1 SE
1	Absent	28.0	28.0	24.1	23.5	22.7	22.0	21.8	21.3	21.0	20.2	19.8	18.7	23.0 ± 0.9
1	Present	31.0	31.0	27.1	26.4	23.2	22.6	22.1	21.6	21.1	20.4	20.2	20.0	23.9 ± 1.2
3	Absent	30.1	30.1	30.1	30.1	30.1	30.0	29.9	29.8	29.6	29.6	29.6	29.5	29.9 ± 0.1
3	Present	32.5	32.0	31.8	30.9	30.5	30.6	30.5	29.9	—	—	—	—	31.1 ± 0.3

[a] Air temperature 1 m above the water surface, under a light breeze, was 31 C at noon (Transect 1) and 33 C at 2 pm (Transect 3).

TABLE 10. *Nutrient content of whole macrophyte shoots sampled in 1977-82 (values are mean percent dry weight ± 1 SE).*[a]

Element	Berchtold's and Sago Pondweeds	Curly-leaf Pondweed	Coontail	Bushy Pondweed	Water Stargrass	Elodea	All Plants
Potassium	0.40 ± 0.08	0.45 ± 0.11	0.73 ± 0.20	0.62 ± 0.25	1.25 ± 0.54	2.03 ± 0.33	0.66 ± 0.09
Phosphorus	0.30 ± 0.01	0.28 ± 0.02	0.35 ± 0.01	0.29 ± 0.03	0.34 ± 0.03	0.48 ± 0.04	0.32 ± 0.01
Nitrogen	2.34 ± 0.08	2.19 ± 0.13	2.44 ± 0.06	2.28 ± 0.08	2.17 ± 0.16	2.37 ± 0.43	2.30 ± 0.05
Sulfur	0.35 ± 0.01	0.32 ± 0.02	0.36 ± 0.01	0.35 ± 0.02	0.31 ± 0.03	0.30 ± 0.01	0.33 ± 0.07
Calcium and magnesium	3.98 ± 0.35	4.57 ± 0.55	3.68 ± 0.12	5.08 ± 0.54	2.67 ± 0.25	5.79 ± 2.14	4.11 ± 0.21
Sample size	20	20	19	8	8	3	78

[a] Bushy pondweed and water stargrass were only analyzed in 1981 and 1982, elodea only in 1982, because of the previous scarcity of these species in the lake. All samples were composites of plant samples randomly selected from each transect on each date.

genus found, but nearly 10 genera were each represented by 2 or 3 species. Insects also accounted for nearly one-half of the total number of individuals collected on the bottom and on plants.

Fly and midge larvae (Diptera) were the most diverse order of insects in the lake (Table 13). Chironomidae were especially speciose, with 21 species in 18 genera. This supports its reputation for considerable adaptive radiation in lakes (Saether 1979). Dragonflies and damselflies (Odonata), beetles (Coleoptera), caddisflies (Trichoptera), and true bugs (Hemiptera) were next most diverse with each order represented in the lake by over 10 species.

Macroinvertebrates other than insects contributed about 30 species to the lake (Table 14). Free-living water mites (Arachnida: Acari), with 9 species in 8 genera, were the most diverse order of noninsect macroinvertebrates. Crustaceans were better represented in plankton samples and were not adequately collected in the benthos.

Burch (1982) was followed for disagreements in nomenclature of snails. *Fossaria* s. str. are lumped under *Lymnaea* by Edmondson (1959) and Pennak (1978). *Physella* is treated as *Physa* by Edmondson (1959), Eddy and Hodson (1961), Te (1975), and Pennak (1978). *Helisoma anceps* Menke is synonymous with *H. antrosa* (Conrad) in Baker (1928) and Eddy and Hodson (1961).

Because many rare species were found in the lake, a much smaller fauna occurred on any particular sampling date. Only 1 or 2 specimens were collected of 37 species. About 40 species were found only once. Some were not aquatic and were probably blown into the lake. They included such true bugs (Hemiptera) as weevils (Curculionidae), stink bugs (Pentatomidae), and aphids (Homoptera: Aphididae). Others were stream inhabitants that washed into the lake after a rain, such as the amphipod *Gammarus* and the mayfly larva *Baetis*.

Many species occurred often in benthic samples, but were seldom abundant (Fig. 24). About 10% to 13% of the taxa comprised at least 5% of the total abundance of organisms, yet about one-half of the taxa occurred in at least 5% of all samples (Table 15). Halverson Lake, therefore, contained many species that survived each year in low numbers. Discounting probable migrants from shore and aquatic species encountered only once or twice, the lake still contained about 100 recurring species typical of lakes or permanent ponds. Since three very different methods were employed, sampling bias cannot likely account for the rareness of so many species. Intense interspecific competition, predation pressure from fishes or invertebrates, and limitations in habitat or niche space could reduce the abundance of many species. Rareness can be adaptive, however, by reducing the encounter frequency with predators and making fuller use of available niches in the lake.

Some taxa dominated all habitats (Tables 16 and 17). Only chironomid larvae were both frequently occurring and abundant in inshore samples. Other abundant taxa included oligochaetes, amphipods (*Hyalella*), mayfly larvae (*Caenis*), damselfly larvae (*Enallagma* and *Ischnura*), dragonfly larvae (*Epitheca*), true bugs (*Neoplea*), caddisfly larvae (*Leptocerus*, *Nectopsyche*, and *Oecetis*), ceratopogonid larvae (*Bezzia* spp. complex), snails (*Helisoma*, *Gyraulus*, and *Physella*), and clams (*Sphaerium*). They formed a guild of 34 species that occurred abundantly and commonly in inshore samples.

The composition of benthos differed among habitats. In midwater (on multiple-plates) relatively more chironomid larvae and amphipods occurred, but there were fewer burrowing mayfly larvae (*Hexagenia*) and clams. A larger percentage of true bugs, dragonfly larvae, and water mites were found on plants, and there was a larger total number of species than found in other habitats sampled. The mean number of taxa/sample, however, was not significantly different among benthos found on plants (14 species), in midwater on multiple-plates (12), and on the bottom near shore (11), when tested with one-way ANOVA. Some macrophyte

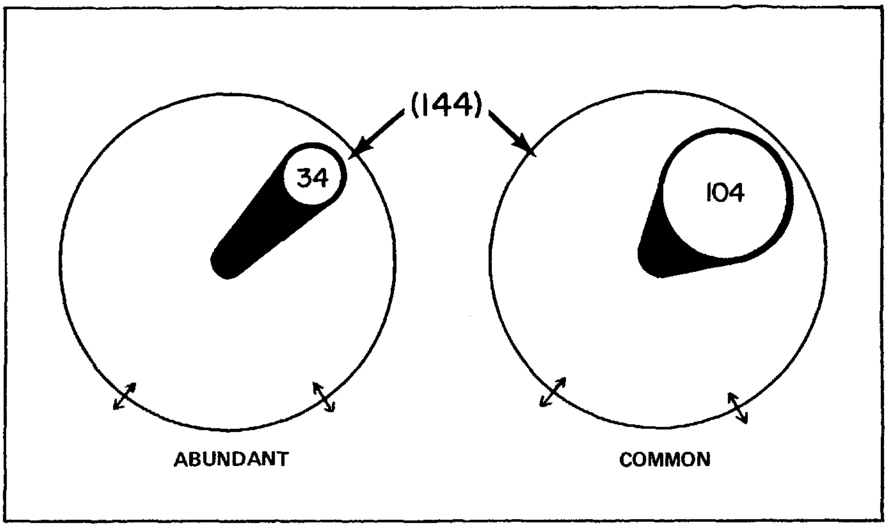

FIGURE 24. *Number of macroinvertebrate species comprising at least 5% of individuals (34 "abundant" species) and samples (104 "common" species). Arrows signify fluctuations in pool sizes through migration or local extinction.*

TABLE 11. *Diversity of macroinvertebrate, zooplankton, and phytoplankton communities of Halverson Lake in 1977-82.*[a]

Parameter	Macro-invertebrates	Phyto-plankton	Zoo-plankton
No. genera	135	80	49
No. species	144	114	72
SW diversity (mean ± 1 SE)	2.4 ± 0.02	2.1 ± 0.08	2.3 ± 0.05

[a] Based on 164 macroinvertebrate samples at Stations 1-5, and 68 phytoplankton and 129 zooplankton samples at Stations B and C.

TABLE 12. *Number of taxa identified in bottom samples and from plants in Halverson Lake in 1977-82.*

	No. Taxa	
Taxon	Insects	Total
Phyla	1	6
Classes	1	10
Orders	9	20
Families	45	68
Genera	108	135
Species	113	144
Individuals (thousands)	498	1,130

TABLE 13. *Insects identified in Halverson Lake in 1977-82.*[a]

Order / Family / Genus Species	Common Name
Ephemeroptera (L)	Mayflies
Caenidae	Squaretails
Caenis sp.	
Ephemerellidae	Spiny crawlers
Ephemerella sp.[b]	
Baetidae	Minnow mayflies
Baetis sp.[b]	
Callibaetis sp.	
Ephemeridae	Burrowing mayflies
Hexagenia limbata (Serville)[2]	
Odonata: Anisoptera	Dragonflies
Aeshnidae	Darners
Aeshna sp.	
Anax sp.	
Boyeria vinosa (Say)	
Cordulliidae	Greeneyed skimmers
Dorocordulia libera Selys	
Epitheca sp.[c]	
Gomphidae	Clubtails
Arigomphus sp.	
Dromogomphus spinosus Selys[b]	Selys
Gomphus sp.	
Stylurus sp.	
Libellulidae	Common skimmers
Celithemis sp.	
Erythemis simplicicollis (Say)[b]	
Leucorrhinia sp.	
Libellula sp.	
Perithemis tenera (Say)	
Plathemis lydia (Drury)[b]	
Sympetrum sp.	
Tramea sp.[b]	
Odonata: Zygoptera	Damselflies
Coenagrionidae	Narrow-winged damselflies
Anomalagrion hastatum (Say)	
Argia sp.[b]	
Coenagrion sp.	
Enallagma sp.	
Ischnura verticalis (Say)	
Nehalennia sp.[b]	
Lestidae	Spreadwinged damselflies
Lestes sp.[b]	
Hemiptera: Heteroptera (L, A)	Aquatic bugs
Belostomatidae	Giant water bugs
Belostoma flumineum Say	
Lethocerus sp.	
Corixidae	Water boatmen
Sigara sp.	
Gerridae	Water striders
Gerris sp.	
Trepobates sp.	
Mesovellidae	Water treaders
Mesovelia mulsanti White	
Naucoridae	Creeping water bugs
Pelocoris femoratus Palisot de Beauvois[b]	
Nepidae	Water scorpions
Ranatra sp.	
Notonectidae	Backswimmers
Buenoa sp.	
Notonecta sp.	
Pentatomidae[b]	Stink bugs
Pleidae	Pygmy backswimmers
Neoplea striola (Fieber)	
Veliidae	Shortlegged striders
Microvelia sp.[b]	
Hemiptera: Homoptera (A)	Leafhoppers and aphids
Aphididae[b]	Aphids
Trichoptera (L)	Caddisflies
Hydroptilidae	Micro caddisflies
Agraylea multipunctata Curtis[b]	
Hydroptila sp.	
Orthotrichia sp.	
Oxyethira sp.	
Leptoceridae	Longhorned case makers
Ceraclea sp.	
Leptocerus americanus (Banks)	
Nectopsyche sp.	
Oecetis sp.	
Setodes sp.	
Triaenodes sp.	
Phryganeidae	Giant case makers
Phryganea sp.[b]	
Polycentropodidae	Tubemakers
Polycentropus sp.[b]	
Psychomyiidae	Nettube caddisflies
Lype diversa (Banks)[b]	
Megaloptera (L)	Alderflies
Sialidae	Alderflies
Sialis sp.	
Neuroptera (L)	Lacewings and spongillaflies
Chrysopidae	Lacewings
Chrysopa sp.[b]	
Lepidoptera (L)	Moths and butterflies
Pyralidae: Nymphulini	Aquatic moths
Coleoptera (L, A)	Beetles
Dytiscidae	Predaceous diving beetles
Coptotomus sp.[b]	
Cybister fimbriolatus (Say)[b]	
Hydroporus sp.	
Hygrotus sp.	
Illybius sp.	
Laccophilus sp.	
Liodessus sp.	
Gyrinidae	Whirligig beetles
Dineutus sp.	
Haliplidae	Crawling water beetles
Haliplus sp.	
Peltodytes sp.	
Chrysomelidae	Leaf beetles
Donacia sp.[b]	
Curculionidae[b]	Weevils
Elmidae	Riffle beetles
Ancyronyx variegatus (Germar)	
Dubiraphia sp.	
Stenelmis sp.	
Helodidae	Marsh beetles
Scirtes sp.[b]	
Hydrophilidae	Water scavenger beetles
Berosus sp.	
Hydrophilus triangularis Say	
Tropisternus sp.	
Diptera (L)	Flies and midges
Stratiomyidae	Soldier flies
Nemotelus sp.	
Odontomyia sp.	
Oxycera sp.[b]	
Tabanidae	Deer flies
Chrysops sp.	
Tabanus sp.	
Ephydridae	Shore flies
Ceratopogonidae	Biting midges
Alluaudomyia sp.[b]	
Atrichopogon sp.[b]	
Bezzia spp. complex[d]	
Chaoboridae	Phantom midges
Chaoborus albatus Johnson	
C. flavicans (Meigen)[b]	
C. punctipennis (Say)	
Chironomidae[e]:	Non-biting midges
Chironominae	
Chironomus attenuatus Walker	
C. plumosus (Linnaeus)	
Dicrotendipes modestus (Say)	

TABLE 13. *(Continued)*

Endochironomus nigricans (Johannsen)	
Glyptotendipes lobiferus (Say)	
Lauterborniella varipennis (Coquille)	
Micropsectra sp.	
Parachironomus sp.	
Paratanytarsus sp.	
Polypedilum sp.	
Tanytarsus sp.	
Chironomidae:	
Orthocladiinae	
Acricotopus sp.[b]	
Nanocladius sp.	
Chironomidae:	
Tanypodinae	
Clinotanypus sp.	
Djalmabatista sp.[b]	
Guttipelopia spp.	
Labrundinia sp.	
Larsia sp.	
Procladius spp.	
Culicidae[b]	Mosquitoes
Tipulidae	Crane flies
Tipula sp.[b]	

[a] Insects were identified from Cook (1956), Hilsenhoff (1975, 1981), Edmunds et al. (1976), and Wiggins (1977). Scientific names and classification followed Brigham et al. (1982); common names followed McCafferty (1981). Life-history stages are noted in parentheses as L (larvae, nymphs, immatures, or pupae) and A (adults).
[b] Only 1 or 2 individuals were found in the lake.
[c] *Epitheca* (Odonata: Corduliidae) included *Epicordulia* and *Tetragoneuria*, following Hilsenhoff (1981).
[d] *Bezzia* complex (Diptera: Ceratopogonidae) included *Bezzia* s. str., *Palpomyia* and *Probezzia*, following Hilsenhoff (1975).
[e] Chironomid genera were identified from Hilsenhoff (1975, 1981); species were identified from Webb and Brigham (1982). The lake may contain other species in the same genera than those listed.

TABLE 14. *Free-living macroinvertebrates, other than insects, identified in Halverson Lake in 1977-82.*[a]

Phylum / Class / Order / Family / Genus Species	Common Name
Coelenterata	Hydras and jellyfishes
Hydrozoa	Hydras
Hydroida (Anthomedusae)	
Hydridae	
Hydra americana Hyman	
Nematoda	Roundworms
Adenophorea	
Enoplida	
Ironidae	
Cryptonchus sp.	
Annelida	Segmented worms
Oligochaeta	Earthworms
Haplotaxida	
Naididae	
Dero digitata (Müller)	
Paranais sp.	
Stylaria lacustris (Linnaeus)	
Tubificidae	
Limnodrilus udekemianus Claparède	
Limnodrilus sp.	
Hirudinea	Leeches
Pharyngobdellida	
Erpobdellidae	
Erpobdella punctata (Leidy)	
Rhynchobdellida	
Glossiphoniidae	
Helobdella triseralis (E. Blanchard)[b]	
Placobdella papillifera (Verrill)	
Arthropoda	Arthropods
Crustacea	Crustaceans
Amphipoda	Scuds
Gammaridae	
Gammarus pseudolimnaeus Bousfield[c]	
Talitridae	
Hyalella azteca (Saussure)	
Decapoda	Crabs and crayfishes
Astacidae	Crayfishes
Cambarus d. diogenes Girard	
Arachnida	Mites, spiders, scorpions
Acari: Trombidiformes[d]	Freshwater mites
Arrhenuridae	
Arrhenurus globator (Müller)	
Axonopsidae	
Albia stationis Thor	
Hydrarchnidae	
Hydrachna sp.	
Hydrodromidae	
Hydrodroma despiciens (Müller)	
Limnesiidae	
Limnesia undulata (Müller)	
Mideopsidae	
Mideopsis americanus (Marshall)	
Pionidae	
Piona cf. *pugilis* (Wolcott)	
P. rotunda (Kramer)	
Unionicolidae	
Neumania semicircularis Marshall	
Mollusca	Mollusks
Gastropoda	Snails
Limnophila	
Lymnaeidae	
Fossaria s. str. cf. *parva* (Lea)	
Physidae	
Physella gyrina (Say)	
P. integra (Haldeman)	
Planorbidae	
Gyraulus (Torquis) *hornensis* Baker	
G. (*T.*) *parvus* (Say)	
Helisoma anceps (Menke)	
Pelecypoda (Bivalvia)	Clams
Heterodonta	
Sphaeriidae	Finger-nail clams
Sphaerium sp.	
Bryozoa (Polyzoa)	Moss animals
Phylactolaemata	Freshwater bryozoans
Lophopodidae	
Pectinatella repens (Linnaeus)	
Plumatellidae	
Plumatella magnifica Leidy	

[a] Macroinvertebrates other than insects were initially keyed to genus with Edmondson (1959), Eddy and Hodson (1961), and Pennak (1978). Further identifications followed Goodey (1963), Ferris et al. (1976), and Tarjan et al. (1977) for Nematoda; Brinkhurst and Jamieson (1971) and Howmiller (1975) for Oligochaeta; Klemm (1972) for Hirudinea; Crocker and Barr (1968) for Astacidae; Wolcott (1902 *in* Edmondson 1959) and Marshall (1921, 1924, 1927, 1933, 1935, 1937, and 1940 *in* Edmondson 1959) for Acari; Baker (1928) and Burch (1982) for Gastropoda; and Burch (1972) for Sphaeriidae.
[b] *Helobdella triseralis* (E. Blanchard) was identified by Donald J. Klemm. The species name lumps *H. fusca* (Castle) and *H. lineata* (Verrill), which could not be separated in the Halverson Lake material (Klemm 1972).
[c] Only a single individual, from a bass stomach, was known from the lake. They were common in streams entering the lake.
[d] Freshwater and some terrestrial mites, formerly considered Hydrachnellae or Hydracarina, are classified here as Trombidiformes, following Edmondson (1959) and Pennak (1978).

TABLE 15. *Percent macroinvertebrate taxa contributing at least 5% of all individuals or samples during 1977-82.*[a]

Contribution of Taxa	Taxa Sampled: Lake Bottom	Submerged Macrophytes	Midwater on Multiple Plates
Total individuals (%)	12	13	10
Total samples (%)	42	60	68
Number of taxa	48	55	41

[a] A single taxon was counted each for Acari, Chironomidae, Hirudinea, Nematoda, and Oligochaeta.

samples supported few benthos, and lowered the mean taxa for all plant nets.

The bottom fauna was less diverse at Station C. It included significantly fewer taxa/sample than did samples from the other bottom sampling stations, when tested with one-way ANOVA. *Chaoborus* dominated at Station C. Some chironomid larvae, oligochaetes, caddisfly larvae, ceratopogonids, and mollusks occurred sporadically in profundal samples. The station was devoid of dissolved oxygen for about 8 months of each year. *Chaoborus* larvae, contributing over 90% of the fauna, could survive there by vertically migrating into the upper oxygenated water column each evening.

Chaoborus punctipennis (Say) dominated at Station C; *C. albatus* Johnson dominated inshore, but occurred there in low numbers. *C. punctipennis* made up 68% of the chaoborids at Station C, 40% at Station B, and less than 15% inshore. A similar inshore-offshore replacement pattern was noted by Roth (1968). These smaller *Chaoborus* species survive fish predation pressure better than do larger species (Pope et al. 1973).

The species richness of Halverson Lake may not be unusual for shallow hard water lakes and permanent ponds in temperate climates. The species pool of aquatic macroinvertebrates can be large for a lake district or local geographical area (Macan 1970, Magnin 1977, Saether 1979). The species of annelids, amphipods, mollusks, and many of the insects found in Halverson Lake are cosmopolitan and regularly occur in Wisconsin lakes (Hilsenhoff and Narf 1968). Peterson and Hilsenhoff (1972) reported over 20 species of Chironomidae on the bottom of Lake Wingra. Schiemer (1979) found 13 chironomid species in the central European lake, Neusiedlersee. Most of the invertebrate genera reported on macrophytes in Clear Lake, Iowa (Mrachek 1966) were also collected in Halverson Lake.

Macroinvertebrate Habitats

Macroinvertebrates occupied diverse habitats. Most species were collected among submerged macrophytes or on the lake bottom inshore, partly because these were large habitats and intensively sampled. Most bottom species occurred on the sediments, but burrowing species were often more abundant. Macroinvertebrates appeared less numerous and diverse on emergent vegetation, in open water, and on the water surface. Floating mats of filamentous algae, underwater brush and tree limbs, and rock crevices formed microhabitats for some invertebrates. The surrounding watershed contributed some rare species. The species richness of the littoral region was due to its habitat diversity, large surface area, abundance of detritus and benthic algae as food, and position as an ecotone between the profundal region and shore.

Few macroinvertebrate species were restricted to a single habitat, but some habitats had a limited fauna (Table 18). Only 13 of 78 species on submerged macrophytes and 6 of 61 bottom species were not sampled elsewhere (Tables 16 and 17). The open water habitat contained 33 swimming and diving species, but only *Chaoborus* and some young chironomid larvae were partly planktonic. Five species occupied the water surface as epipleuston, but only *Dineutus* whirligig beetles ever became abundant. Seven species regularly occupied algal mats (McCafferty 1981, Merritt and Cummins 1984), especially pygmy backswimmers (*Neoplea*). Floating mats trapped detritus and supported sessile protozoans, rotifers, and diatoms. They established microhabitats for benthos before vascular plants became widespread. Algal mats appeared to serve as feeding stations for some benthos, until summer water temperatures above 30 C restricted their use.

Faunal exchanges occurred among habitats. Loss of vegetation in the fall meant that many species had to occupy the lake bottom, such as amphipods, pygmy backswimmers, and water mites. Species exchanges also occurred offshore, as *Chaoborus* larvae migrated between the lake bottom and upper water column each day. Diel migrations of invertebrates between the bottom and plants were not studied.

Species composition differed between the bottom and macrophytes. The plants supported relatively more *Physella* snails, water mites, amphipods, naidid oligochaetes, damselfly and dragonfly larvae, true bugs, aquatic moths, *Leptocerus* caddisfly larvae, and beetles. Among chironomid larvae, *Glyptotendipes* and *Lauterborniella* were more common on plants than the bottom. The lake bottom contained a higher proportion of *Gyraulus* snails, tubificid oligochaetes, finger-nail clams, and larvae of chironomids and ceratopogonids. Burrowing species were more abundant on the bottom than the plants. *Chironomus*, *Dicrotendipes*, *Micropsectra*, and *Procladius* were common chironomids on the lake bottom in winter (Table 19). *Chironomus, Dicrotendipes*, and *Procladius* were also common on both plants and the bottom in summer. Despite a broad overlap in species, the lake bottom and submerged macrophytes held differing compositions of macroinvertebrates.

Bottom Fauna

The distribution and abundance of bottom fauna in Halverson Lake varied seasonally. The inshore stations supported the largest number and diversity of macrobenthos during most of the 41 sampling dates.

In June, July, and August nearly three-fourths of all bottom fauna occurred beneath the macrophytes (Fig. 25). About 60% of chironomid larvae and over 90% of snails, clams, and larvae of caddisflies, damselflies, dragonflies, and mayflies occurred in the littoral region. Their abundance dropped at Station B (Fig. 2), just outside the macrophytes. Station C, having thermally stratified, was devoid of dissolved oxygen during summer and, thus, supported fewer organisms.

In cooler months about 50% of all bottom fauna were found inshore. This percentage decrease was due to a large recovery of bottom fauna at Station C, rather than to a real decline in abundance inshore. Increased water circulation during spring and fall overturn replenished the concentration of dissolved oxygen at Station C and permitted a larger bottom fauna. The fauna may have migrated from shore, because the station was situated near

TABLE 16. *Percentage of samples containing macroinvertebrates from different habitats in 1977-82.*

PHYLUM / Class / Order / Suborder / Family	Genus	Midwater on Multiple Plates	Plant Dwellers	Bottom: Inshore	Bottom: Stn. B	Bottom: Stn. C
COELENTERATA (hydras)	*Hydra*	10	0	1	0	0
NEMATODA (roundworms)		1	5	1	0	0
ANNELIDA (segmented worms)		78	64	84	80	43
Oligochaeta (earthworms)		35	57	80	80	43
Hirudinea (leeches)		61	34	21	0	0
ARTHROPODA		100	100	100	100	100
Crustacea						
Amphipoda (scuds)	*Hyalella*	99	93	41	5	0
Insecta		100	100	100	100	100
Ephemeroptera (mayflies)		98	84	73	0	0
Baetidae	*Callibaetis*	19	12	1	0	0
Caenidae	*Caenis*	98	81	73	0	0
Ephemeridae	*Hexagenia*	0	0	1	0	0
Odonata: Zygoptera (damselflies)		80	74	37	0	0
Coenagrionidae	*Coenagrion*	1	7	0	0	0
	Anomalagrion					
	Enallagma	72	57	12	0	0
	Ischnura					
	Nehalennia	0	0	1	0	0
Odonata: Anisoptera (dragonflies)		31	39	27	0	0
Aeshnidae	*Anax*	5	7	0	0	0
Corduliidae	*Epitheca*	22	13	11	0	0
Gomphidae		0	9	12	0	0
	Arigomphus	0	7	5	0	0
	Dromogomphus	0	0	3	0	0
	Gomphus	0	2	1	0	0
	Stylurus	0	1	5	0	0
Libellulidae		4	12	7	0	0
	Celithemis	2	1	0	0	0
	Erythemis	0	0	1	0	0
	Leucorrhinia	0	11	0	0	0
	Libellula	0	3	4	0	0
	Perithemis	1	1	3	0	0
	Sympetrum	0	2	1	0	0
Hemiptera (true bugs)		19	36	7	0	0
Belostomatidae	*Belostoma*	0	2	0	0	0
	Lethocerus					
Corixidae	*Sigara*	0	2	0	0	0
Gerridae	*Trepobates*	0	1	0	0	0
Helodidae		0	1	0	0	0
Nepidae	*Ranatra*	2	2	0	0	0
Notonectidae		0	6	0	0	0
	Buenoa	0	3	0	0	0
	Notonecta	0	3	0	0	0
Pleidae	*Neoplea*	19	27	7	0	0
Trichoptera (caddisflies)		81	99	87	51	46
Hydroptilidae		11	0	1	0	0
	Hydroptila	8	0	0	0	0
	Orthotrichia	0	0	1	0	0
	Oxyethira	1	0	1	0	0
Leptoceridae		78	99	87	51	46
	Ceraclea	7	4	0	0	0
	Leptocerus	39	73	55	20	19
	Nectopsyche	61	39	79	49	35
	Oecetis	8	27	12	0	0
	Triaenodes	8	10	2	0	0
Megaloptera (alderflies)						
Sialidae	*Sialis*	0	2	1	0	0
Lepidoptera (moths)		0	14	0	0	0
Coleoptera (beetles)		75	69	19	0	0
Curculionidae		0	1	0	0	0
Dytiscidae		54	28	2	0	0
	Coptotomus	1	0	0	0	0
	Hydroporus	8	18	1	0	0
	Laccophilus	2	7	0	0	0
	Liodessus	47	9	2	0	0
Elmidae		6	0	3	0	0
	Ancyronyx	0	0	2	0	0
	Dubiraphia	1	0	1	0	0
	Stenelmis	5	0	0	0	0
Gyrinidae	*Dineutus*	11	2	0	0	0
Haliplidae		0	51	10	0	0
	Haliplus	0	27	10	0	0
	Peltodytes	0	40	1	0	0
Hydrophilidae		19	18	8	0	0
	Berosus	19	16	8	0	0
	Hydrophilus	1	0	0	0	0
	Tropisternus	1	3	0	0	0
Diptera (flies and midges)		100	86	100	100	100
Ceratopogonidae		61	45	90	85	24
Chaoboridae	*Chaoborus*	17	5	23	88	100
Chironomidae		100	83	100	100	95
Ephydridae		0	5	0	0	0
Stratiomyidae		0	4	0	0	0
	Nemotelus	0	3	0	0	0
	Odontomyia	0	1	0	0	0
Tabanidae		0	8	19	0	0
	Chrysops	0	8	16	0	0
	Tabanus	0	0	3	0	0
Arachnida (mites and spiders)						
Acari (free-living water mites)		49	68	55	34	14
MOLLUSCA (snails and clams)		94	100	100	100	76
Gastropoda (snails)		94	100	100	93	70
Lymnaeidae	*Lymnaea*	0	13	1	0	0
Physidae	*Physella*	82	95	94	39	22
Planorbidae	*Helisoma*	47	95	84	61	49
	Gyraulus	71	93	96	73	49
Pelecypoda (clams)	*Sphaerium*	25	82	98	100	30
Total no. samples		83	107	242	41	37

TABLE 17. *Percent of total number of macroinvertebrates comprising at least 1% of those collected in different habitats in 1977-82.*

PHYLUM Class Order Suborder Family	Genus	Midwater on Multiple Plates	Plant Dwellers	Bottom Inshore	Bottom Stn. B	Bottom Stn. C
ANNELIDA		2	11	5	14	1
Oligochaeta		1	10	5	14	1
Hirudinea		1	1	tr	0	tr
ARTHROPODA		94	61	47	49	99
Crustacea: Amphipoda	*Hyalella*	18	17	tr	tr	0
Insecta		75	40	46	48	99
Ephemeroptera		7	3	1	0	0
Caenidae	*Caenis*	7	2	1	0	0
Odonata		2	1	tr	0	0
Coenagrionidae	*Anomalagrion* *Enallagma* *Ischnura*	2	1	tr	0	0
Trichoptera		7	16	13	3	1
Leptoceridae	*Leptocerus*	tr[a]	14	3	tr	tr
	Nectopsyche	7	2	10	2	tr
Coleoptera		tr	2	tr	0	0
Haliplidae	*Peltodytes*	0	1	tr	0	0
Diptera		58	17	31	46	98
Ceratopogonidae		1	1	5	3	tr
Chaoboridae	*Chaoborus*	tr	tr	tr	12	91
Chironomidae		57	16	26	31	7
Arachnida: Acari	*Arrenhurus* *Hydrodroma* *Limnesia* *Piona* spp. *Neumania*	2	4	tr	tr	tr
MOLLUSCA		3	28	49	37	1
Gastropoda		2	25	31	5	1
Physidae	*Physella*	1	13	5	1	tr
Planorbidae	*Helisoma*	tr	6	7	2	1
	Gyraulus	1	6	19	3	tr
Pelecypoda	*Sphaerium*	1	3	18	32	tr
Organisms sampled (1000's)		20	10	—	—	—
(1000's/m^2)		—	—	5,070	360	610

[a] tr = less than 0.50%.

TABLE 18. *Habitat preferences of macroinvertebrates in Halverson Lake, as reported in the literature. Data are percentage of total number of organisms sharing each habitat.*

	Habitats in Which Organisms Taken				
Habitat Preference	Midwater on Multiple Plates	Plant Dwellers	Bottom Inshore	Bottom Stn. B	Bottom Stn. C
Crawling-burrowing					
Bottom sediments	2	13	28	50	1
Sediments, macrophytes	76	44	62	37	8
Macrophytes	21	41	11	2	1
Swimming					
Midwater	1	1	tr	12	91
Lake surface	tr[a]	tr	0	0	0

[a] tr = less than 0.5%.

the dam and down current from the other stations.

During ice-free times Station B contained about one-fourth of the mean number of macrobenthos found at the four inshore stations. The absence of vascular macrophytes at Station B may have discouraged colonization of benthos that depended on the detritus and epiphytic algae associated with the macrophytes. The sediments at Station B may have been too fine and sorted for certain case-building larvae. Loss of benthos just outside the littoral region was also observed in Polish lakes (Wiśniewski and Dusoge 1983). Submerged macrophyte foliage, although present mainly in warmer months, appeared necessary for the full development of a bottom fauna in the lake.

The bottom fauna was most abundant in winter (Fig. 26). Chironomids were abundant as late instar larvae. Mollusks and water mites were less abundant in winter, but many plant-dwelling species occurred on the bottom in winter. Winter was a relatively stable period for benthos. Waves and strong currents were gone, water temperature was nearly constant, and the bottom appeared homogeneous with the loss of macrophyte foliage. Winter losses of benthos from emergence cannot occur under the ice cover. The cold water probably slowed larval development in some species, and reduced predation pressure from other invertebrates and fishes (especially bass). Despite the loss of macrophyte foliage, bottom samples held more macroinvertebrates in winter.

The number of offshore benthos changed dramatically on some dates (Fig. 27). Huge numbers of *Chaoborus* larvae appeared at Station C in February and spring 1981. Since each triplicate haul of the Ekman dredge on three successive dates was crammed with the larvae, sampling and counting errors could be ruled out. Clear ice and early ice-out may have shortened the period of bottom oxygen depletion and reduced mortality of larvae.

The total catch from multiple-plate samplers was less variable than bottom or plant samplers. Total numbers were not significant among inshore stations or samplers within stations, when tested with one-way ANOVA. The multiple-plate samplers were populated with chironomid, mayfly, and caddisfly larvae (Fig. 28). Sample sizes increased in fall, from a build-up of *Nectopsyche* caddisfly larvae, and dropped in spring, when chironomids emerged from the lake. Such population changes appeared more clearly on multiple-plate samplers, because patterns of bottom dispersal can partly mask such changes in Ekman dredge samples.

The bottom fauna was more diverse inshore than offshore (Table 20). The Shannon-Weaver diversity index for inshore samples (2.4 $\pm$ 0.02) was significantly larger than that for Station C samples (1.2 $\pm$ 0.1), as tested with one-way ANOVA on log-transformed data. No significant differences were found in diversity among inshore stations, when similarly tested. Station B values (2.1 $\pm$ 0.5) were intermediate. Percent evenness was 71% inshore and at Station B, but only 50% at Station C, because of the predominance of one taxon (*Chaoborus*) at Station C. The inshore stations supported both a richer fauna and a more balanced composition than the offshore stations.

Association With Macrophytes

Bottom macroinvertebrates were more diverse and numerous under submerged macrophytes. Mean taxa/sample was significantly greater on the bottom inshore (11 taxa) than at Stations B (7) or C (5). No significant differences were found among all inshore sta-

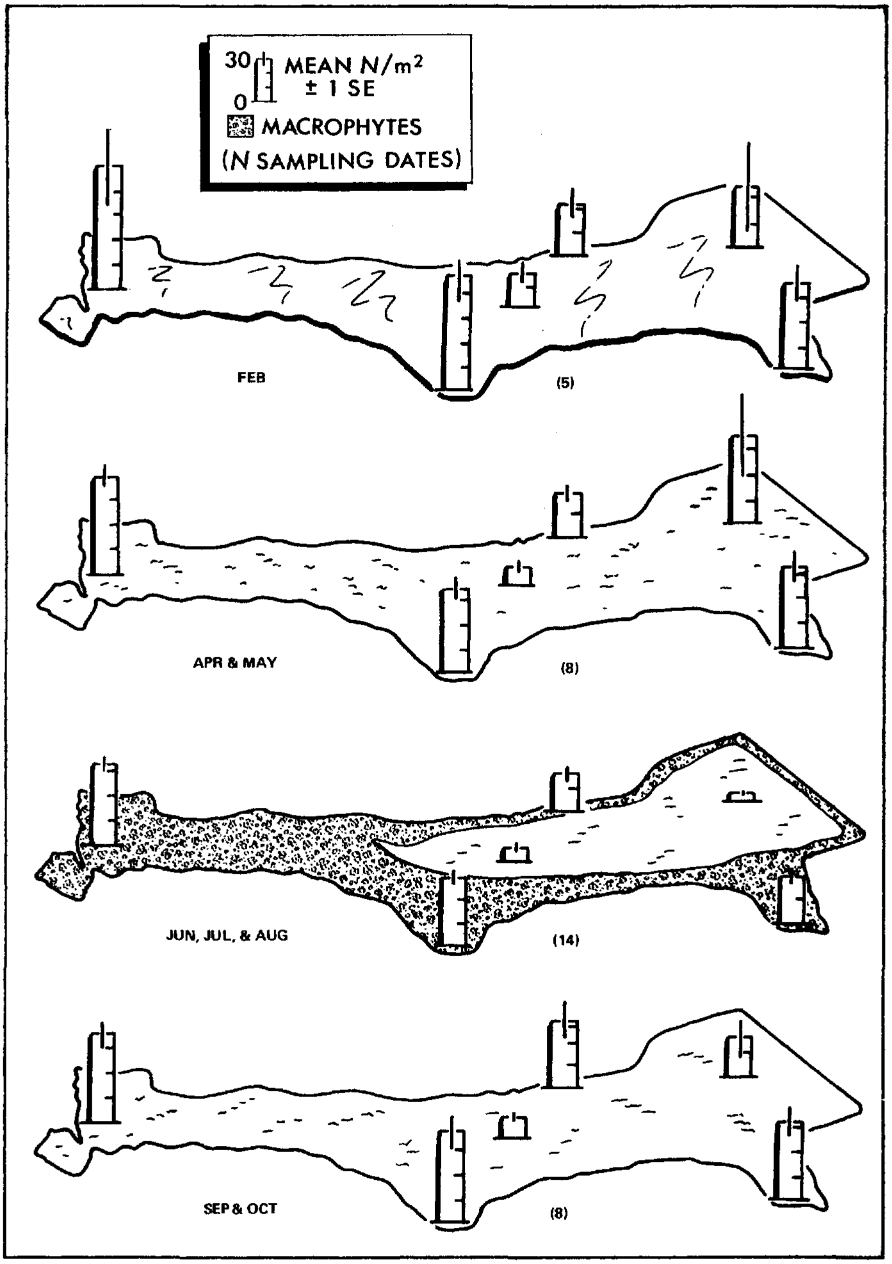

FIGURE 25. *Seasonal changes in mean density of bottom macroinvertebrates at six locations.*

TABLE 19. *Percentage of the total number of non-biting midge larvae (Diptera: Chironomidae) collected on the lake bottom, February 8, 1981.*

	Sampling Station			
Taxon	Inshore	B	C	Total
Chironominae				
Chironomus spp.	19	100	92	40
Dicrotendipes modestus	45	0	0	33
Endochironomus nigricans	0	0	1	1
Glyptotendipes lobiferus	2	0	0	2
Micropsectra sp.	7	0	0	5
Tanypodinae				
Clinotanypus sp.	1	0	0	1
Guttipelopia sp.				
Procladius spp.	25	0	0	20
Total no. larvae identified	99	25	12	136
Total no. larvae sampled	733	93	12	838

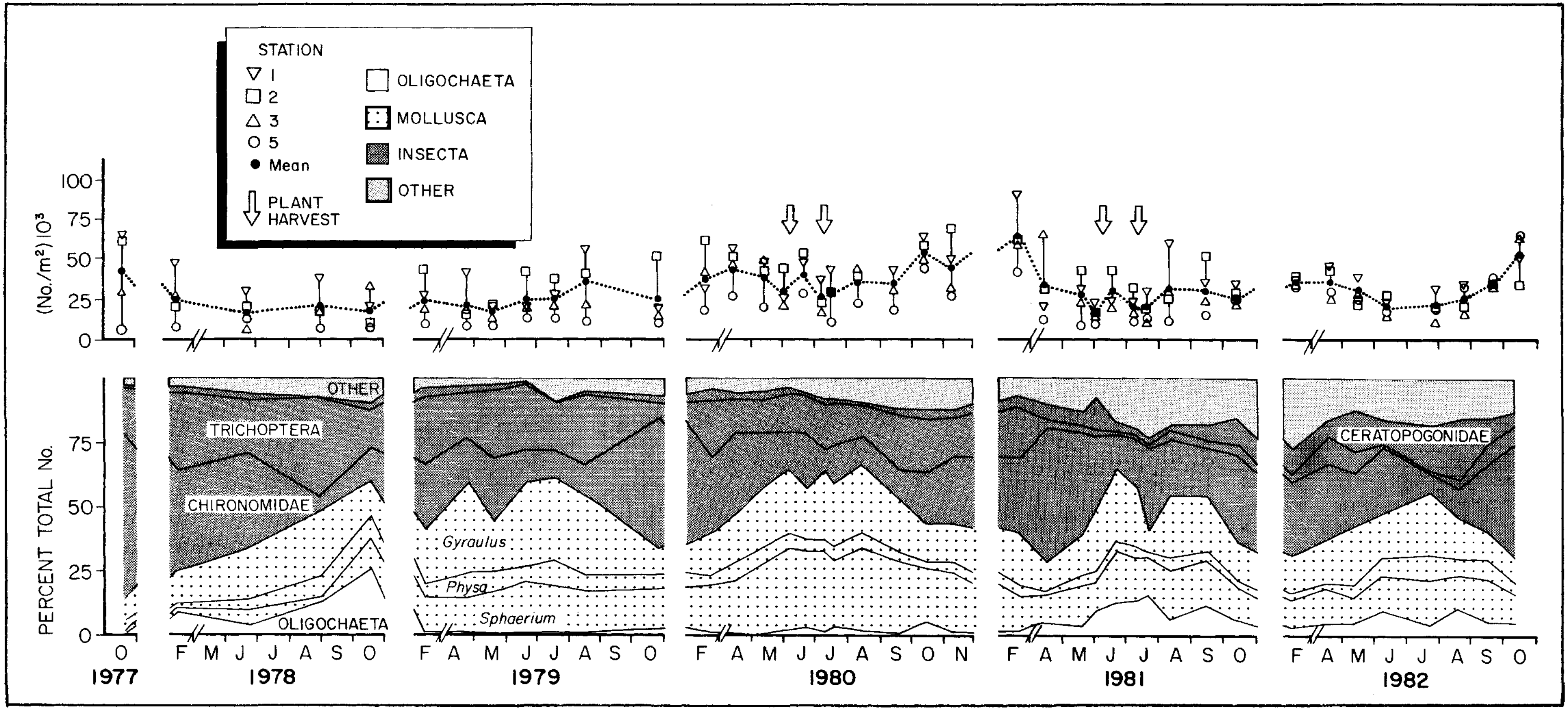

FIGURE 26. *Total abundance and relative frequency of macroinvertebrates in inshore Ekman dredge samples. A dotted line joins the mean abundance of the four stations. Arrows denote the plant harvests.*

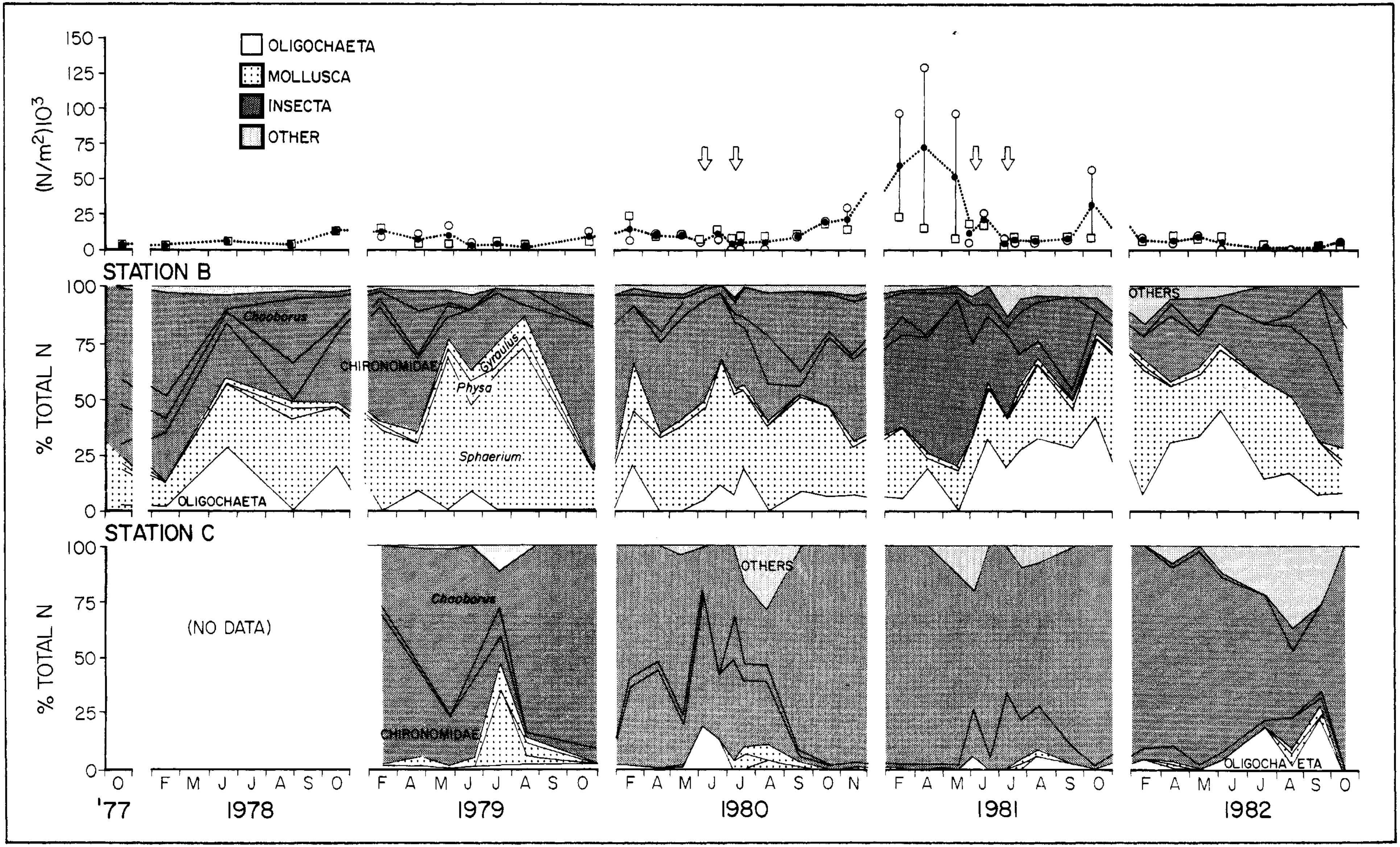

FIGURE 27. *Macroinvertebrate catches in offshore bottom samples.*

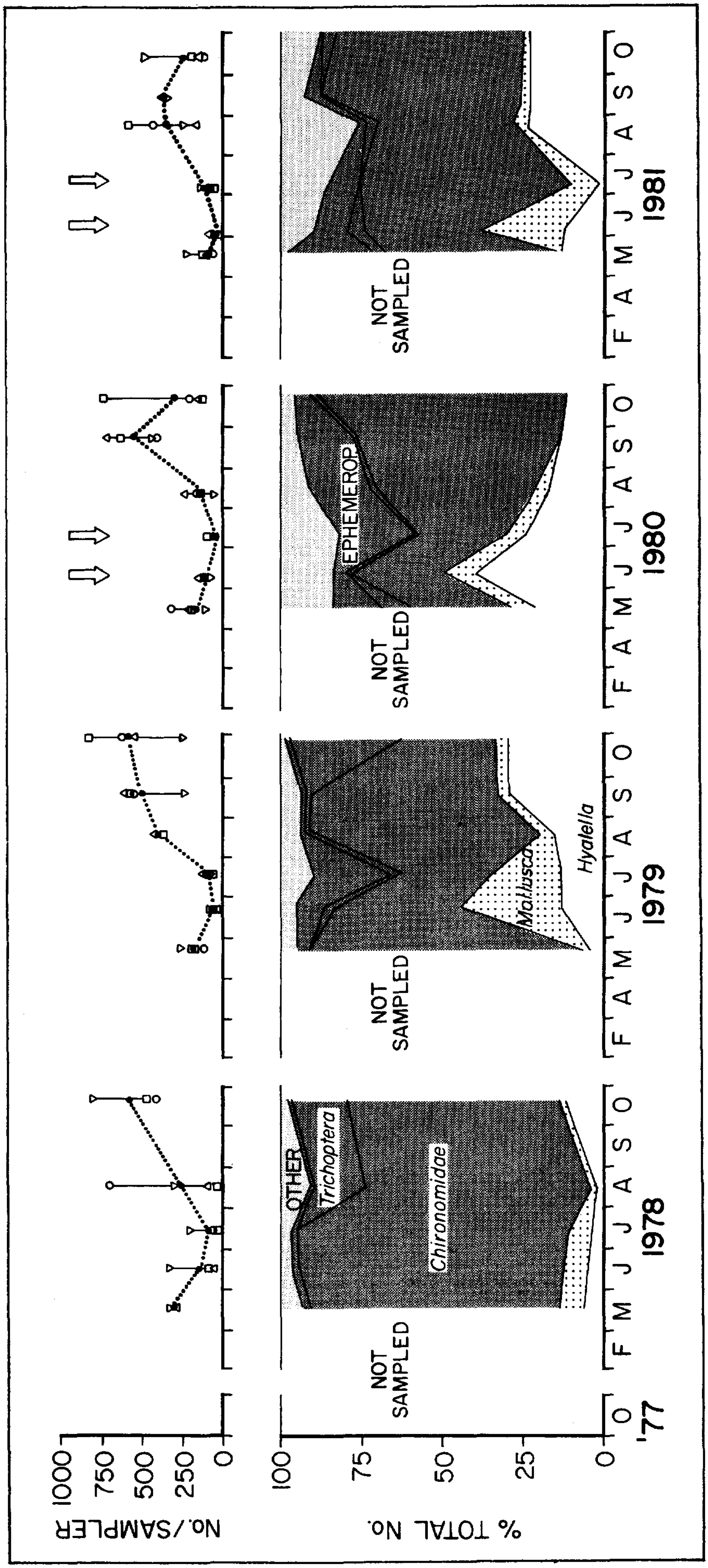

FIGURE 28. *Macroinvertebrate catches in midwater on multiple-plates. The samplers were not worked in winter.*

tions in number of taxa, when tested with one-way ANOVA. Station 5, however, had significantly fewer benthos than Stations 1 and 2, until it became vegetated with water stargrass in 1982 (Fig. 26).

The number of benthos was not directly associated with plant biomass. No significant product-moment correlations were found between macrophyte biomass and the number of total benthos, Chironomidae, finger-nail clams, or Trichoptera in inshore bottom dredge samples. The amount of living foliage was not as important to bottom organisms as perhaps the accumulation of dead organic matter in sediments beneath the plants.

Submerged macrophytes supported a more abundant and richer bottom fauna in other lakes. Snails, chironomid larvae, and oligochaetes were more abundant beneath sago pondweed in an Iowa lake (Tebo 1955). *Tanytarsus* and *Cryptochironomus* increased beneath *Chara* in a Michigan lake (Beatty and Hooper 1958). Spread of potamogetons in Lake Kariba, Zambia increased the number of benthos by 60% (McLachlan 1969). Soft bottom areas of well-vegetated European lakes support high benthic populations (Schiemer et al. 1969).

The benthos were more varied on the submerged macrophytes than on the lake bottom. More taxa occurred on plants (55 taxa) than in bottom samples (48) or midwater multiple-plate samples (41). Several co-dominant and many rare taxa were found on plants. At least 70% of the samples from plants contained *Hyalella* amphipods, snails, chironomid larvae, *Leptocerus* caddisfly larvae, finger-nail clams, naidid oligochaetes, and *Caenis* mayfly larvae (Table 16).

The total number of macroinvertebrates on plants did not differ significantly among sampling dates or macrophyte species (Fig. 29), when tested with one-way ANOVA. Samples in June and July 1980-82 averaged 31 ± 6 organisms/g dry weight of plant (after subtracting the catch in control nets). Sample variances were large and influenced by some control nets with large catches.

Water stargrass averaged 16 ± 8 organisms/g. Its flat linear foliage ranked lowest in branching for dominant species in the lake (Fig. 30). Highly branched plants have relatively larger surface areas and support more invertebrates (Krecker 1939, Andrews and Hasler 1943, Mrachek 1966, Kořinková 1971, Voigts 1976), even as plastic imitations of real plants (Gerrish and Bristow 1979). The spread of water stargrass in Halverson Lake after 1981 may, therefore, have meant a reduction in plant-dwelling benthos over previous years.

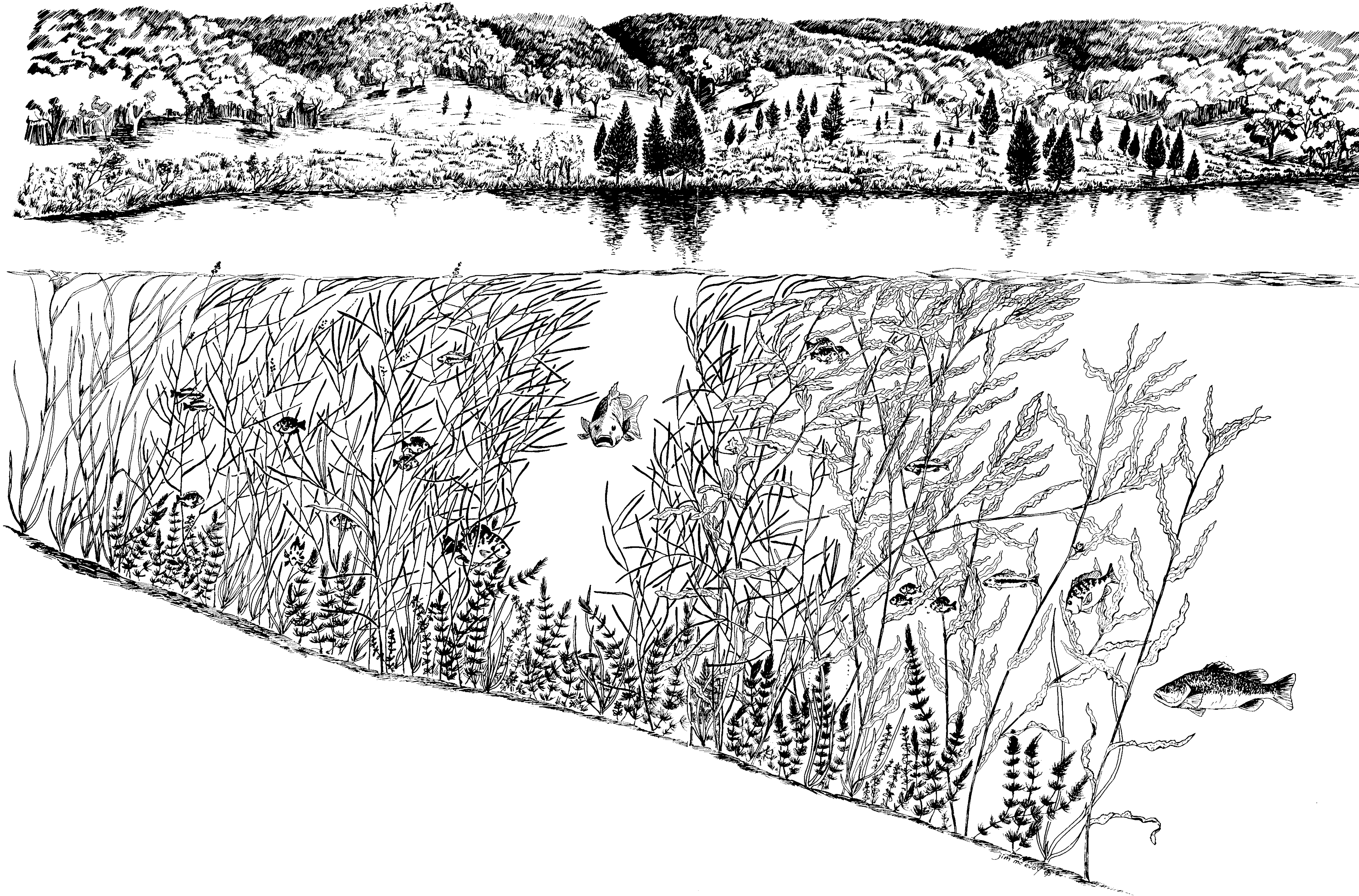

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TABLE 20. *Diversity of macroinvertebrates sampled on plants, in midwater on multiple plates, and on the bottom. Data are pooled for all sampling stations and dates in 1977-82.*

Parameter	Plant Nets	Multiple Plate Samplers	Ekman Dredges: Inshore	Ekman Dredges: Stn. B	Ekman Dredges: Stn. C
Sample mean ± 1 SE					
No. taxa/sample	13.8 ± 1.1	11.8 ± 0.2	11.0 ± 0.2	7.5 ± 0.2	4.8 ± 0.3
SW diversity index ($\log_2$)	2.3 ± 0.1	1.9 ± 0.1	2.4 ± 0.02	2.1 ± 0.05	1.2 ± 0.1
Evenness (%)	65 ± 3	54 ± 2	71 ± 2	72 ± 2	52 ± 5
Total of all samples					
No. samples	107	83	164	41	37
No. taxa	55	41	48	21	13

TABLE 21. *Diversity of macroinvertebrates on macrophytes sampled in June and July 1980-82.*

Parameter	Berchtold's Pondweed	Bushy Pondweed	Curly-leaf Pondweed	Water Stargrass	Coontail	Water Milfoil	Chara	Elodea
Sample mean ± 1 SE								
No. taxa/sample	18.6 ± 2.0	15.5 ± 8.5	15.0 ± 2.3	13.0 ± 2.5	12.8 ± 2.1	12.0 ± 4.6	12.0 ± 3.8	9.7 ± 3.0
SW diversity index	2.8 ± 0.2	2.4 ± 0.4	2.7 ± 0.2	2.7 ± 0.2	1.7 ± 0.2	2.3 ± 0.2	2.1 ± 0.3	2.0 ± 0.2
Evenness (%)	66 ± 3	65 ± 3	71 ± 5	74 ± 1	48 ± 5	67 ± 3	71 ± 12	67 ± 13
Total of all samples								
No. samples	25	6	21	9	18	7	11	10
No. taxa	24	24	21	16	18	19	20	14

Macroinvertebrates were usually more diverse on Berchtold's pondweed (18.6 ± 2.0 taxa/sample) than on other plant species (Table 21). Mean Shannon-Weaver diversity indices (2.3 ± 0.1) and number of taxa/sample (13.8 ± 1.1) for all samples were not significantly different, when tested with one-way ANOVA. Mean evenness was about 65% for most samples, indicating that at least several taxa dominated the fauna. Chironomid larvae and some larvae of caddisflies, damselflies, dragonflies, mayflies, and biting midges comprised about 40% of the total catch on plants. Live snails accounted for one-third of the fauna. The remaining organisms were mostly naidid oligochaetes and amphipods. Krecker (1939) found a similar dominance by chironomid larvae and naidid oligochaetes on submerged macrophytes.

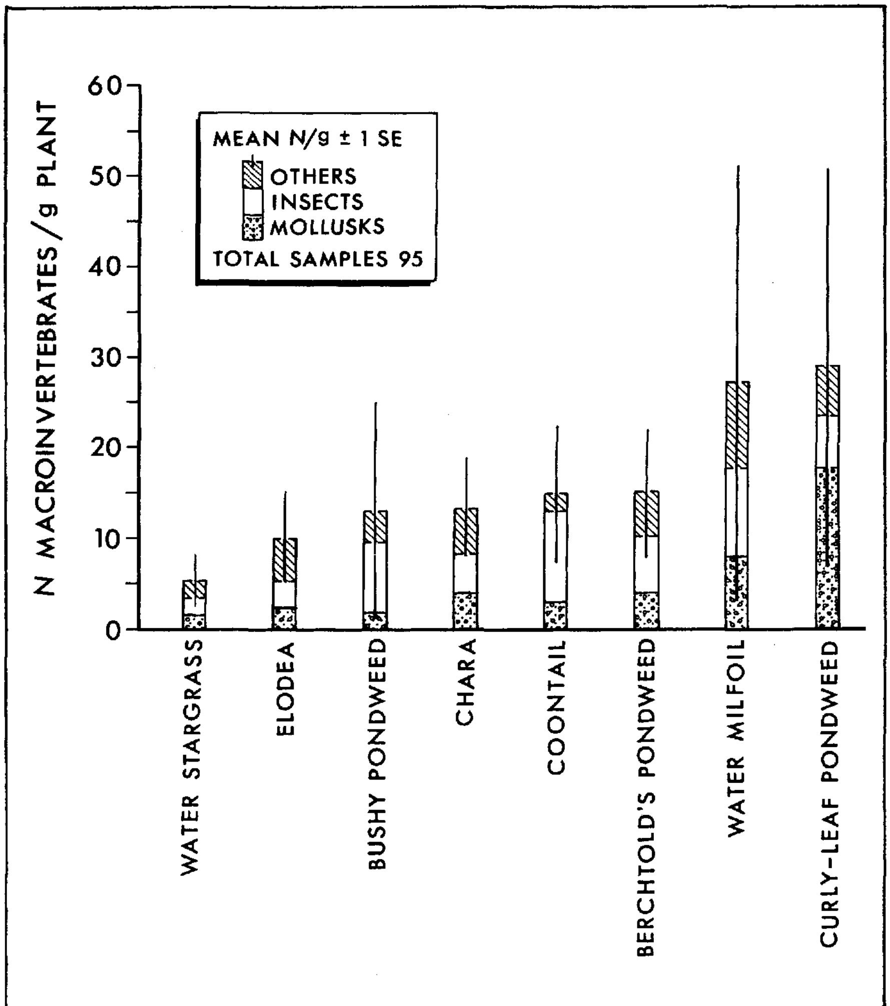

FIGURE 29. *Total density of macroinvertebrates on plants harboring different macrophyte species. Data are pooled for June-August 1979-82.*

Food of Macroinvertebrates

Over three-fourths of macroinvertebrates in the littoral region of Halverson Lake consume detritus and algae (Table 22), based on literature reports. Few species feed entirely on live plants or animals. Carnivores often ingest detritus and carrion. Only some caddisfly and moth larvae in the lake pierce plant tissues for food. Most plant-dwellers graze detritus, diatoms, and microbenthos on macrophytes. Few predators, therefore, could be classified

TABLE 22. *Food habits of macroinvertebrates in Halverson Lake for 1977-82, as reported in the literature. Data are percentage of organisms sharing each food category.*

Major Food	Midwater on Multiple Plates	Plant Dwellers	Bottom Inshore	Bottom Stn. B	Bottom Stn. C
Detritus	1	10	5	14	1
Algae, detritus	78	76	83	66	7
Algae, macrophytes	tr[a]	2	tr	0	0
Live animals, carrion	5	8	6	13	91
Live animals, detritus	16	5	6	8	2

[a] tr = less than 0.50%.

as strictly detrictivores, herbivores, or carnivores.

The food habits of insects in Halverson Lake were mainly drawn from Hungerford (1948), Cummins (1973), Edmunds et al. (1976), Merritt and Cummins (1984), and Brigham et al. (1982). The diet of macroinvertebrates other than insects came from Edmondson (1959), Barnes (1974), and Pennak (1978). These reports were supplemented by direct examination of the foregut contents of many chironomid larvae, nematodes, and annelids from Halverson Lake.

Plant-dwelling chrironomid larvae mostly contained diatoms or detritus in their gut, but Tanypodinae larvae ingested cladocerans or ostracods with detritus (Table 23). The detritus consisted of mineral grains and black partially digested matter. Empty diatom shells, cladoceran carapaces, or mineral grains were frequently found in the hindgut of chironomid larvae. Slow digestion or evacuation of these items may have inflated their importance in the diet. Mineral grains may have been accidentally swallowed or specifically ingested to macerate diatom shells and chitinous exoskeletons.

Reliance on detritus ultimately lengthens food chains by requiring a decomposer step. Lindeman (1942) recognized the importance of detritus and placed bacterial decomposers at the center of food cycle relationships in bog lakes. Benthic macro-decomposers may be just as important in hard water lakes. Settling of detritus in still water places a premium on benthic feeding. Open-water feeding may be more important in streams, where detritus can remain longer in suspension (Cummins 1974).

Senescing macrophytes were the largest source of detritus in Halverson Lake. The shared use of such an abundant resource diminished competition and permitted coexistence of many different species. The macroinvertebrate community partly functioned to convert dead organic matter into a form more palatable to fishes and other carnivores. Energy and materials would otherwise be lost from the predator-prey food web.

Numerous feeding strategies have evolved among macroinvertebrates. Most macrobenthos in Halverson Lake were collectors and shredders (Table 24). Suspension- and filter-feeders and general food gatherers were grouped under collectors. They included some chironomids (Chironominae and Orthocladiinae), clams, annelids, and *Ceraclea* caddisfly larvae. Plant chewers and shoot miners were considered shredders. They included some chironomids, *Leptocerus* and *Nectopsyche* caddisfly larvae, moth larvae, and snails. *Baetis, Callibaetis,* and *Caenis* mayfly larvae were scrapers of attached algae and detritus. Snails variously used scraping, collecting, and shredding to ingest food. Collectors, shredders, and scrapers were widespread and included most benthic species.

Nine species of macroinvertebrates fed directly on macrophytes. These plant piercers bored into plant shoots and pumped out the plant tissues. They were seldom abundant (Table 24) and included water boatmen (*Sigara*), hydrophilid caddisfly larvae, and larvae of haliplid and hydrophilid beetles.

Carnivorous macroinvertebrates included animal piercers and engulfers. Predation can be selective for size and species of prey consumed (Cooper 1983) and include stalking or active pursuit of prey. Twenty-two species were animal piercers and 39 species were engulfers. Some leeches, most true bugs (except *Sigara*), dytiscid beetle larvae, *Chaoborus* larvae, and water mites were primarily animal piercers.

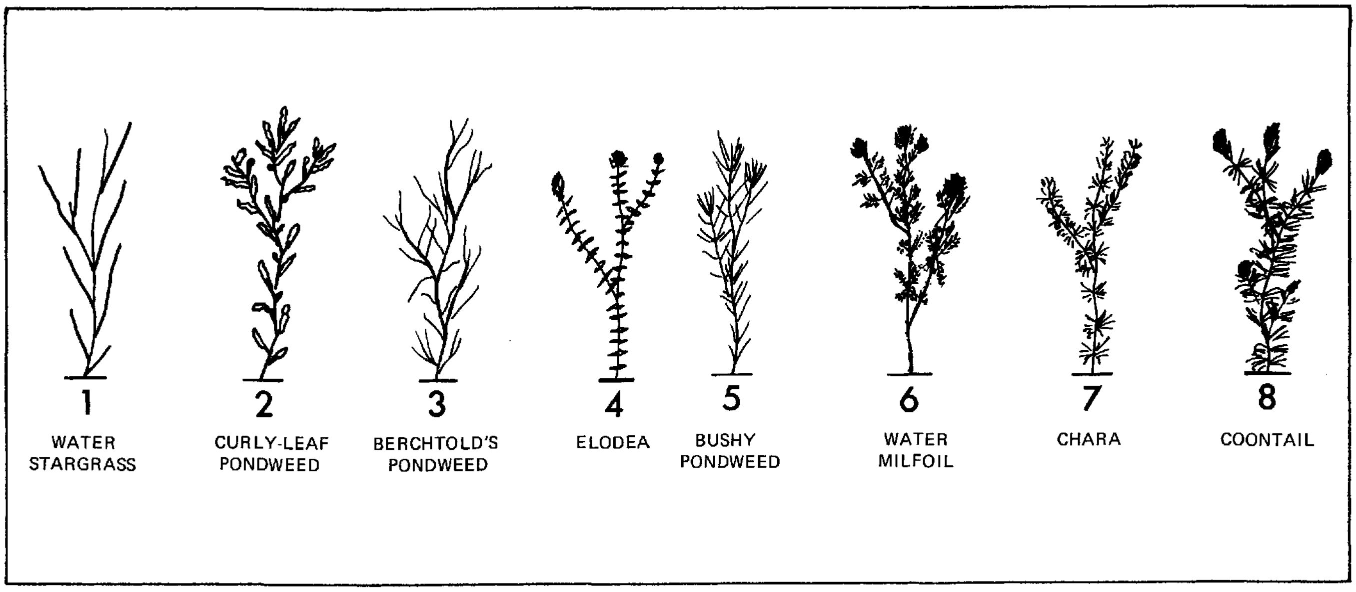

FIGURE 30. *Branching of dominant submerged macrophytes. Sago and Berchtold's pondweeds shared the same rank in branching.*

TABLE 23. *Abundance and gut contents of non-biting midge larvae (Diptera: Chironomidae) found on macrophytes.*[a]

Taxon	Total No. (Frequency of Occurrence) Berchtold's Pondweed	Curly-leaf Pondweed	Coontail	Major Gut Content[b]
Chironominae				
Chironomus attenuatus	0	0	6 (1)	Detritus
Dicrotendipes modestus	5 (3)	1 (1)	0	Detritus
Endochironomus nigricans	0	0	1 (1)	Detritus, diatoms
Glyptotendipes spp.	4 (3)	4 (3)	4 (2)	Diatoms
Lauterborniella varipennis	2 (2)	1 (1)	3 (1)	Diatoms, detritus
Parachironomus sp.	0	1 (1)	0	Detritus
Polypedilum sp.	0	1 (1)	0	Diatoms
Orthocladiinae				
Acricotopus	1 (1)	0	0	Diatoms
Tanypodinae				
Guttipelopia spp.	1 (1)	1 (1)	0	Ostracods
Larsia sp.	0	1 (1)	1 (1)	Detritus, cladocerans
Procladius spp.	2 (1)	3 (1)	1 (1)	Cladocerans, detritus
No. larvae (no. samples)	15 (4)	13 (4)	16 (4)	—

[a] The chironomid larvae were collected in plant nets at Stations 1 and 2 on June 1-9, 1980.
[b] The dominant item in each gut is listed first; detritus refers to mineral grains usually mixed with dark organic matter.

Most damselfly and dragonfly larvae, *Oecetis* caddisfly larvae, alderfly larvae (*Sialis*), whirligig beetles (*Dineutus*), hydrophilid beetle larvae, and larvae of ceratopogonids and Tanypodinae chironomids were mainly engulfers. *Chaoborus* larvae could pierce or engulf prey, depending on size of prey.

These feeding strategies are generalized functional responses. They are labels for complex and highly evolved feeding behaviors. Underlying such feeding strategies are differences in size of prey ingested (Cummins 1973), specialized mouth parts, and different behaviors (Merritt and Cummins 1984, Cooper 1983). They enable food and space to be more efficiently partitioned.

TABLE 24. *Feeding strategies of macroinvertebrates in Halverson Lake for 1977-82, as reported in the literature. Data are the percentage of organisms employing each feeding strategy.*

Feeding Strategy[a]	Midwater on Multiple Plates	Plant Dwellers	Bottom Inshore	Bottom Stn. B	Bottom Stn. C
Detritus-algae feeding					
Collecting	57	41	40	66	6
Shredding	15	42	47	11	3
Scraping	7	3	1	0	0
Plant feeding					
Macrophyte piercing	tr[b]	1	tr	0	0
Animal feeding					
Piercing	4	6	1	13	91
Engulfing	17	7	12	11	2

[a] Terms adopted from Merritt and Cummins (1984).
[b] tr = less than 0.5%.

FISH USE OF HABITAT AND FOOD

Distribution and Activity

The littoral region during summer supported a large concentration of fishes. The fishes, mostly bass and bluegills of ages 0-II, broadly overlapped in distribution and partially segregated by size. Those under 120 mm (ages 0-I) occurred in vegetation near shore; larger ones dispersed more widely and occurred offshore. Few fishes, however, were observed in the ankle-deep water along shore. Fish fry (5-10 mm length) first appeared in bass stomachs in early June, but were difficult to see and net during electrofishing and were rarely caught until fall. Some were observed among macrophytes, but others may have moved offshore in June and July (Beard 1982).

The pelagic region in summer was occupied by crappies of all sizes and by bass and bluegills above 179 mm (over age II). They were typically caught just outside the macrophyte beds during the day. Bluegills of 120-180 mm (ages I-III) were more common in the littoral region than were bass of this size range. They moved inshore to feed and spawn. Crappies rarely moved inshore during the day and comprised less than 10% of electrofishing catches during summer. Crappies, consequently, were less dependent on littoral habitat in summer and remained more spatially segregated from bass and bluegills.

The fish community dispersed in cooler months. Bass over 180 mm and crappies of all sizes were mostly electrofished inshore during spring and fall. Crappies over 120 mm moved inshore in early spring; smaller ones were more common there in fall. Anglers only caught bluegills and crappies in winter.

Fish activity was best observed in spring and early summer, when the lake water was clear (Secchi disk greater than 3.5 m). Activity was also assessed by comparing day and night catches from angling, beach seining, and electrofishing. Diel differences in stomach fullness were clued to feeding activity, assuming a 50% reduction in stomach content within 4-8 hours (Seaburg and Moyle 1964, Windell 1967).

Fishes were most active during the day, partly because they relied on sight and could see better during the day than at night. Bass and crappies exhibited a burst of feeding activity near dawn and dusk, when angling was most effective. Eighteen percent of bass stomachs were empty in day catches, compared with less than 10% of bluegill and crappie stomachs.

Access to Macrophytes

Submerged macrophytes functioned as a screen to selectively restrict fish movements (Fig. 31). Plant beds exceeding 300 g/m^2 (dry weight) were usually devoid of fishes, as were dense canopies of sago pondweed. Monotypic stands of water stargrass and curly-leaf pondweed, over 200 g/m^2, were difficult for fishes to penetrate. Such dense islands of vegetation, contributing nearly 15% of all plant samples in June-August, acted as refuges for macroinvertebrates escaping fish predation. Fishes under 120 mm (ages 0-I) readily penetrated the remaining plant beds. By distributing their foliage throughout the water column, even dense stands of Berchtold's pondweed appeared loose under water and allowed small fishes access to the foliage.

Larger bass (over 180 mm and over age II) were uncommon in macrophyte beds, until die-back of curly-leaf pondweed created channels for them to cruise in (Fig. 9). Other channels were formed by boats, muskrats, plant harvesting, runoff from shore, and senescence of other plants. Bass 180-550 mm (ages II-IX) were electrofished in such channels. Cool spring water on the bottom moderated summer water temperatures in parts of these channels. As other pondweeds deteriorated in August, openings and channels progressively widened and the foliage became less selective to fishes. Fishes then increased in the diet of bass, suggesting that macrophytes became less effective as sanctuaries for small fishes.

Plant harvesting and the invasion of water stargrass altered the impact of the macrophyte community on fishes. Plant harvesting, by suddenly removing surface foliage and channelizing the plant beds, temporarily destroyed the plant community as a fish sanctuary and screen. Fishes used the new channels as cruising lanes in search of fish fry. The spread of water stargrass, however, had an opposite effect on fishes. Enormous beds of the plant after 1981 mostly restricted small fishes to looser surrounding vegetation. Because water stargrass grew densely into September and October, large fishes were restricted from inshore areas for about two months longer than in the preharvesting years.

Submerged macrophytes attract multitudes of fishes in other lakes. Bluegills often congregate near vegetation during the day (Keast et al. 1978, Werner et al. 1981). By so grouping, fishes can mutually watch for predators and dart for cover when warned. Plants both obstruct the field of view of fish predators and interfere with their pursuit of fry (Glass 1971). Bluegills often move between open water and plant beds around dawn and dusk (Baumann and Kitchell 1974), but become more solitary, less active, and widely dispersed at night (Stuntz 1975). Individual fish are a smaller target than a school and, remaining motionless at night, can use their lateral line system to detect vibrations of an approaching predator. The protection avoided by plant beds and the sensory capabilities of fishes are often so effective that predators have difficulty finding fish prey.

Annual Diet

Fish stomachs were collected on 55 days from August 1977 through September 1982. Food data from successive days were later combined to give 44 sampling dates. Four dates, occurring within a few days of plant harvesting, were treated separately to avoid harvester effects on diet caused by water turbidity and habitat disturbances. Calculations for the six years, therefore, were based on 40 sampling dates.

Stomachs were examined from 688 bass, 664 bluegills, and 176 crappies on the 40 dates (Table 25). The population structure differed among the three pooled samples. Bluegills and crappies were similar in mean length and weight, but bass averaged 20-25% longer and 50-55% heavier than either

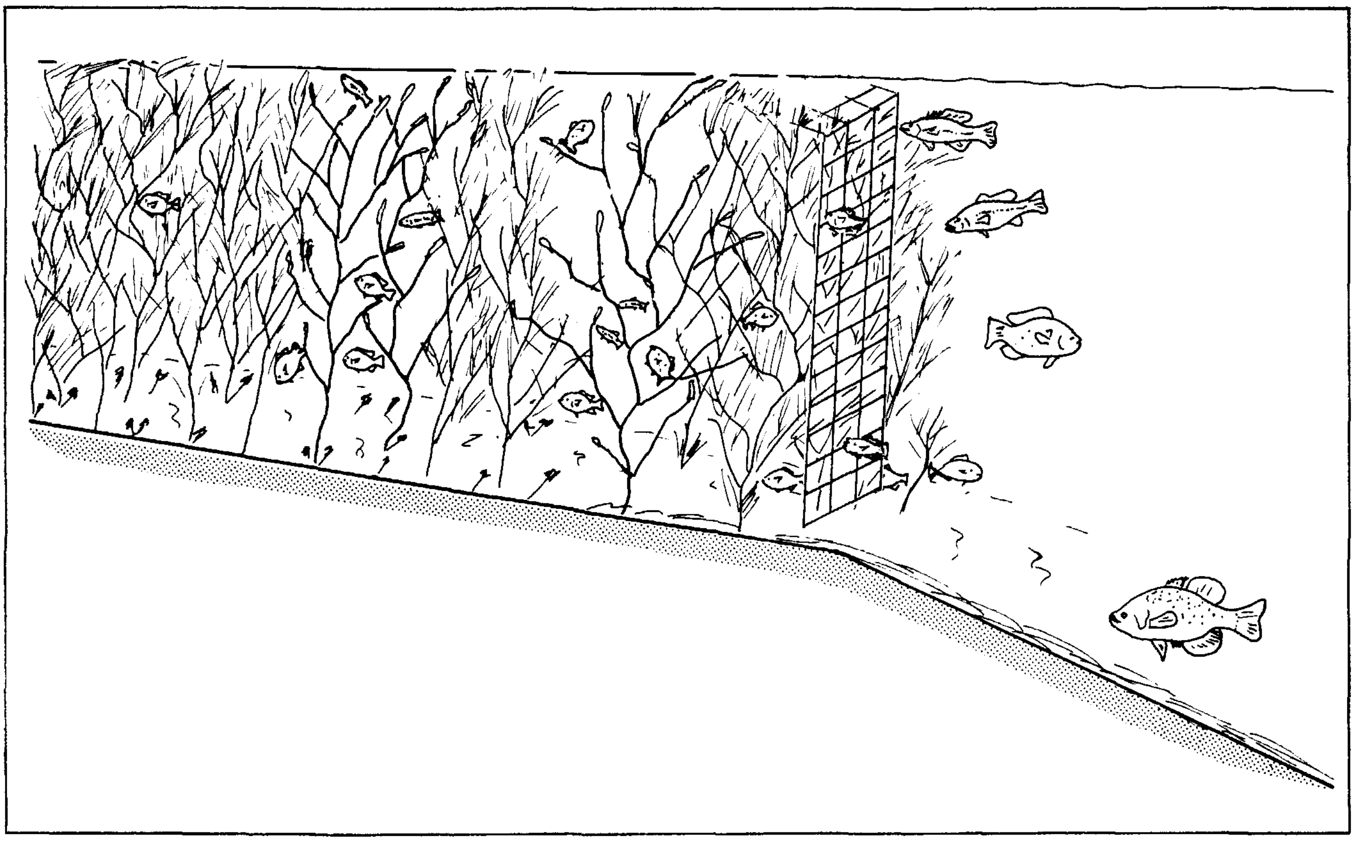

FIGURE 31. *A macrophyte bed depicted as a "selective fish screen" in midsummer. Berchtold's pondweed, some curly-leaf pondweed, and basal shoots of coontail are diagrammed.*

species. Nearly one-third of bass exceeded 200 mm. Maximum length was 487 mm for bass, 307 mm for bluegills, and 289 mm for crappies. Bluegills had the highest mean condition factor. Over 40% of bluegills had a condition factor above 2.0, compared to less than 2% of bass and crappies. Only 20% of bass and bluegills exceeded age II, compared to 10% of crappies.

The fish community selectively shared and partitioned food resources in Halverson Lake. Nearly all species of microcrustaceans (cladocerans, copepods, and ostracods) and about 70% of macroinvertebrate taxa sampled during the six years became prey. Only 20 taxa were regularly eaten by all fish species. They included chironomid larvae, cladocerans, copepods, and fish fry. These foods were segregated more by predator size than by species. Other prey were less commonly shared and became selectively vulnerable to a particular fish species. Thus, snails were primarily consumed by larger bluegills, *Chaoborus* larvae were mainly eaten by crappies, and insects on the water surface were preferred by bass. Plant matter was ingested chiefly by bluegills, although trace amounts appeared frequently in bass stomachs. Most food resources, therefore, were partitioned among the fish community, resulting in a broad range of prey consumed and a multiplicity of energy pathways leading to secondary production by fishes.

Bass principally ate chironomids, odonates, mayflies, fishes, and cladocerans (Table 26). Insects comprised one-half of all items and appeared in 60% of stomachs with food. Chironomid larva and pupae accounted for nearly one-third of both stomachs and items. Odonates and mayflies each appeared in about one-fourth of stomachs with food, but contributed less than 10% of all items. Numerous winged odonates and other flying insects suggest surface feeding. Age 0 fishes appeared in one-third of stomachs but comprised less than 10% of items. *Daphnia* were eaten by 4% of bass with food and accounted for one-fourth of items (Table 27).

The bluegill diet was more diversified. Insects were consumed by 89% of bluegills with food, but contributed one-fourth of all items (Table 26). Chironomid larvae contributed 18% of all items; mayfly, caddisfly, and odonate larvae each accounted for less than 5% of the diet. Both bass and bluegills ate twice as many damselfly as dragonfly larvae, but bluegills ate few winged adults. One-half of bluegills consumed microcrustaceans, but these accounted for nearly three-fourths of all items. *Daphnia*, *Leptodora*, and *Simocephalus* were the main crustaceans eaten. Bluegills supplemented their diet with bryozoans, snails, water mites, and vegetation.

Crappies mainly ate zooplankton (Table 27), including *Daphnia* (67% of

TABLE 25. *Size, condition factor, and age (mean ± 95% CL) of fishes examined for stomach content on 40 dates in 1977-82.*

Parameter	Bass	Bluegill	Crappie
Length (mm)	146 ± 6	110 ± 3	120 ± 8
Weight (g)	87 ± 15	39 ± 4	43 ± 9
Condition (K)	1.3 ± 0.02	1.9 ± 0.03	1.4 ± 0.4
Age (no. annuli)	1.4 ± 0.1	1.8 ± 0.1	1.2 ± 0.2
No. fish	688	664	176

TABLE 26. *Percent occurrence (%FO) and relative abundance (%No.) of major prey in fish stomachs for 40 dates in 1977-82.*

	Bass		Bluegill		Crappie	
Food Category[a]	%FO	(%No.)	%FO	(%No.)	%FO	(%No.)
Crustacea	11	(34)	51	(73)	86	(93)
Amphipoda	6	(1)	22	(1)	18	(tr)
Cladocera	7	(30)	37	(71)	74	(78)
Copepoda	3	(3)	11	(2)	49	(13)
Ostracoda	1	(tr)	16	(tr)	31	(1)
Acari	tr[b]	(tr)	11	(tr)	6	(tr)
Mollusca	2	(tr)	18	(tr)	1	(tr)
Gastropoda	2	(tr)	16	(tr)	1	(tr)
Gyraulus	0	(0)	6	(tr)	tr	(tr)
Physella	1	(tr)	7	(tr)	tr	(tr)
Insecta	60	(55)	89	(23)	88	(7)
Ephemeroptera	21	(8)	39	(1)	23	(tr)
Caenis	7	(2)	34	(1)	15	(tr)
Callibaetis	15	(6)	8	(tr)	5	(tr)
Odonata	25	(5)	23	(tr)	6	(tr)
Anisoptera	7	(3)	9	(tr)	2	(tr)
Zygoptera	12	(2)	16	(tr)	4	(tr)
Hemiptera	13	(4)	5	(tr)	5	(tr)
Sigara	5	(1)	1	(tr)	4	(tr)
Trichoptera	3	(2)	36	(2)	13	(tr)
Leptocerus	1	(1)	16	(1)	10	(tr)
Nectopsyche	2	(tr)	14	(tr)	2	(tr)
Oecetis	1	(tr)	10	(tr)	2	(tr)
Coleoptera	3	(1)	12	(tr)	2	(tr)
Diptera	33	(35)	83	(19)	86	(7)
Ceratopogonidae	3	(1)	27	(1)	23	(tr)
Chaoboridae	3	(1)	9	(tr)	51	(3)
Chironomidae	29	(31)	80	(18)	73	(3)
Fish eggs, flesh, scales	37	(8)	3	(1)	12	(tr)
Plant matter	17	(—)	21	(—)	6	(—)
No. fish sampled (prey x 10^3)	688	(7)	664	(128)	176	(129)
Percent stomachs with food	82		95		93	

[a] Only prey consumed by at least 5% of any fish species was included in this table.
[b] tr = less than 0.5% occurrence or number.

stomachs with food), *Mesocyclops* (46%), and *Leptodora* (18%). Microcrustaceans comprised 90% of all items (Table 26). Insects, chiefly dipteran larvae, occurred in 88% of stomachs with food, but accounted for only 7% of all items. The crappie diet, consequently, was more specialized for zooplankton feeding than that of bass and bluegills.

Bass stomachs averaged 10 prey, compared with 192 for bluegills and 730 for crappies (Table 28). Bass ate one-tenth as many insects as bluegills or crappies. Their stomachs were emptier and they appeared to have fed earlier in the morning.

Relative importance values revealed considerable overlap in diet between bass and bluegills (Table 29). Insects, especially chironomid larvae, were almost equally important in bass and bluegill stomachs, but much less important to crappies. Microcrustaceans were 5 times as important in crappie as bass stomachs and 1.5 times that in bluegill stomachs. *Chaoborus* larvae were mainly important to crappies. Bass and bluegills were mainly insectivores feeding additionally on zooplankton or fish fry, whereas crappies were predominantly zooplanktivores consuming some benthic insects.

TABLE 27. *Percent occurrence (%FO) and relative abundance (%No.) of cladocerans and copepods eaten by fishes on 40 dates in 1977-82.*

	Bass		Bluegill		Crappie	
Food Category[a]	%FO	(%No.)	%FO	(%No.)	%FO	(%No.)
Cladocera						
Bosmina	tr[b]	(tr)	1	(tr)	3	(1)
Ceriodaphnia	0	(0)	1	(tr)	2	(tr)
Chydorus	tr	(tr)	3	(tr)	3	(1)
Daphnia	4	(25)	27	(70)	67	(73)
Eurycercus	1	(tr)	2	(tr)	tr	(tr)
Leptodora	1	(1)	7	(3)	18	(3)
Pleuroxic	0	(0)	1	(tr)	1	(tr)
Simocephalus	3	(3)	8	(1)	5	(tr)
Copepoda						
Diacyclops	tr	(tr)	tr	(tr)	7	(1)
Eucyclops	tr	(tr)	1	(tr)	1	(tr)
Mesocyclops	3	(2)	tr	(tr)	46	(11)
Skistodiaptomus	0	(0)	1	(tr)	12	(1)

[a] *Alona, Diaphanosoma,* and *Macrocyclops* were consumed in trace amounts by a few bass and bluegills.
[b] tr = less than 0.5% occurrence or number.

TABLE 28. *Major prey consumed per 10 fish stomachs on 40 dates in 1977-82 (mean number ± 1 SE).*

Food Category	Bass	Bluegill	Crappie
Crustacea	34 ± 11	1400 ± 190	6790 ± 1280
Amphipoda	1 ± 0.4	12 ± 2	5 ± 1
Cladocera	30 ± 11	1365 ± 183	5674 ± 1280
Copepoda	3 ± 2	33 ± 11	962 ± 211
Ostracoda	tr[a]	8 ± 1	67 ± 12
Acari	tr	2 ± 0.4	1 ± 0.2
Mollusca	tr	8 ± 1	tr
Gastropoda	tr	7 ± 1	tr
Gyraulus	0	2 ± 0.5	0
Physella	tr	3 ± 0.8	tr
Insecta	56 ± 8	446 ± 30	502 ± 83
Ephemeroptera	8 ± 1	26 ± 3	8 ± 5
Caenis	2 ± 0.6	24 ± 3	7 ± 5
Callibaetis	6 ± 1	1 ± 0.3	1 ± 0.2
Odonata	5 ± 0.5	9 ± 1	1 ± 0.2
Anisoptera	3 ± 0.4	3 ± 0.6	tr
Zygoptera	2 ± 0.3	6 ± 1	1 ± 0.2
Hemiptera	4 ± 0.8	1 ± 0.2	1 ± 0.3
Sigara	1 ± 0.2	tr	1 ± 0.2
Trichoptera	2 ± 1	31 ± 6	3 ± 0.8
Leptocerus	1 ± 1	16 ± 6	2 ± 0.8
Nectopsyche	tr	9 ± 2	tr
Oecetis	tr	5 ± 1	tr
Coleoptera	1 ± 0.4	4 ± 1	1 ± 0.5
Diptera	36 ± 8	374 ± 29	479 ± 83
Ceratopogonidae	1 ± 0.1	12 ± 2	1 ± 2
Chaoboridae	1 ± 0.4	7 ± 2	225 ± 43
Chironomidae	31 ± 8	351 ± 30	225 ± 71
Fish eggs, flesh, scales	8 ± 1	21 ± 21	2 ± 0.7
Total no.	101 ± 26	1922 ± 485	7303 ± 2837

[a] tr = 0.5 mean prey per stomach.

Seasonal Changes in Diet

Bass usually ate a greater food volume in spring or fall; bluegills consumed more prey in summer (Figs. 32 and 33). Chironomids comprised the bulk of all fish diets in spring. They accounted for one-third of bass and crappie diets and 40-60% of the bluegill diet. Bluegills in early summer grazed chironomid larvae and *Daphnia* and then switched to a variety of littoral prey. Their diet overlapped that of small bass resident among macrophytes. Food consumption by bass dropped in July of most years, suggesting that bass then had difficulty foraging inshore. Their mean food volume increased 1.5 times after July, as they consumed more fish fry. The diets of all species usually declined after September.

Daphnia were heavily grazed by crappies and bluegills. Bluegills over 50 mm turned in June to feed on littoral macrobenthos, while smaller ones and crappies continued to consume pelagic zooplankton. Crappie stomachs in June contained a mean of 1,800 ± 650 *Daphnia*, almost 4 times the mean number consumed in April. Crappies shifted to eating *Chaoborus* larvae after June, as the number of *Daphnia* dwindled in the lake (Fig. 45).

Fish Size and Diet

Access to macrophyte beds and fluctuations in zooplankton altered food relationships among fishes. Small bass and bluegills (38-119 mm) mainly consumed prey in midwater or on the bottom and plants (Table 30). Larger bass consumed more prey from the water surface, whereas larger bluegills fed almost exclusively in midwater. Crappies fed predominantly in midwater throughout life, but turned increasingly to benthos with age.

Small bass and bluegills were mainly insectivores; crappies remained zooplanktivores until they reached about 200 mm (Fig. 34). Few microcrustaceans were eaten by bass over 80 mm. Insects and fishes were both important to medium (120-179 mm) bass, but fishes outnumbered insects when bass exceeded 240 mm. Bluegills ate

TABLE 29. *Relative importance values (mean ± 1 SE) of major prey consumed by fishes per sampling date in 1977-82. Percent of dates when prey were consumed is in parentheses.*

Food Category	Bass		Bluegill		Crappie	
Crustacea	14 ± 2	(80)	37 ± 4	(95)	51 ± 4	(94)
Amphipoda	2 ± 0.5	(50)	5 ± 0.5	(80)	3 ± 0.8	(35)
Cladocera	7 ± 2	(48)	24 ± 3	(95)	30 ± 3	(94)
Copepoda	2 ± 0.7	(32)	3 ± 0.6	(60)	15 ± 3	(61)
Ostracoda	tr[a]	(12)	3 ± 0.6	(65)	7 ± 1	(58)
Acari	tr	(8)	3 ± 0.6	(58)	2 ± 0.8	(26)
Mollusca	1 ± 0.3	(20)	4 ± 0.6	(68)	tr	(3)
Gastropoda	tr	(18)	4 ± 0.6	(65)	tr	(tr)
Gyraulus	0	(0)	1 ± 0.3	(42)	tr	(tr)
Physella	1 ± 0.4	(12)	2 ± 0.6	(48)	tr	(tr)
Insecta	63 ± 3	(100)	56 ± 3	(98)	38 ± 3	(75)
Ephemeroptera	15 ± 2	(98)	9 ± 0.9	(88)	7 ± 1	(68)
Caenis	3 ± 0.8	(42)	8 ± 1	(85)	6 ± 1	(58)
Callibaetis	11 ± 2	(85)	2 ± 0.4	(55)	1 ± 0.3	(13)
Odonata	15 ± 1	(95)	7 ± 0.7	(82)	1 ± 0.6	(23)
Anisoptera	8 ± 1	(78)	2 ± 0.4	(52)	1 ± 0.6	(10)
Zygoptera	7 ± 1	(70)	4 ± 0.7	(72)	tr	(13)
Hemiptera	7 ± 1	(88)	1 ± 0.2	(48)	3 ± 1	(26)
Sigara	3 ± 0.7	(50)	tr	(20)	2 ± 1	(23)
Trichoptera	1 ± 0.4	(32)	8 ± 0.8	(90)	3 ± 0.9	(26)
Leptocerus	tr	(8)	3 ± 0.6	(62)	2 ± 0.7	(19)
Nectopsyche	1 ± 0.3	(18)	3 ± 0.6	(52)	1 ± 0.5	(10)
Oecetis	tr	(2)	2 ± 0.4	(45)	1 ± 0.5	(13)
Coleoptera	2 ± 0.8	(32)	3 ± 0.6	(62)	1 ± 0.5	(13)
Diptera	21 ± 3	(95)	28 ± 2	(98)	32 ± 2	(94)
Ceratopogonidae	2 ± 0.5	(25)	5 ± 0.6	(82)	6 ± 1	(45)
Chaoboridae	4 ± 2	(28)	3 ± 0.8	(52)	13 ± 2	(77)
Chironomidae	19 ± 3	(90)	26 ± 2	(98)	19 ± 2	(90)
Fish eggs, flesh, scales	21 ± 3	(95)	tr	(5)	2 ± 0.9	(32)
Plant matter	—	(75)	—	(68)	—	(23)
No. sampling dates	40		40		31	

[a] tr = less than 0.5 relative importance value or percent of dates with prey.

progressively more microcrustaceans until about 180 mm, when they mainly ate insects. Microcrustaceans, therefore, were chiefly important to small bass, medium bluegills, and most crappies.

Specific prey shifted in importance as fishes became larger (Table 31). Chironomid larvae became less important to bass and bluegills, but more important to larger crappies. Medium bass took larger insects, such as odonates, true bugs, and mayfly larvae. Bluegills switched to *Daphnia* and eventually *Chaoborus* larvae with size. Crappies progressed to larger zooplankton species (Table 32). *Daphnia* remained important to all crappies, but small fish concentrated on *Bosmina* and *Mesocyclops*, while large crappies grazed *Leptodora*, *Chaoborus*, and chironomids. Over 80% of foods were under 2 mm in small crappies, but over 5 mm in large ones. Electivity indices suggested nonselective feeding by small crappies, but avoidance of prey under 1 mm by large ones (Table 33). They also appeared to select against cyclopoid copepodids of 1-2 mm, but these swift prey can sense fish movements and evade attack (Drenner et al. 1978). By segregating zooplankton prey by size, coinhabiting crappies could reduce intraspecific competition.

TABLE 30. *Relative frequency of habitats used for feeding by fishes during mid-May through August 1977-79, based on prey habitat preferences.*

Prey Habitat	Bass	Bluegill	Crappie
Fish under 120 mm			
Bottom or plants	36	52	2
Midwater	63	48	98
Water surface	1	tr[a]	0
Fish 120-179 mm			
Bottom or plants	56	5	2
Midwater	33	95	97
Water surface	12	tr	tr
Fish over 180 mm			
Bottom or plants	44	6	17
Midwater	38	94	83
Water surface	18	tr	tr

[a] tr = less than 0.5% fish using habitat.

Smaller fishes had a more varied diet than larger ones (Table 34). Small bluegills and crappies ate about twice as many taxa as large ones, but little change was noted in bass. Small bluegills ingested over 50 taxa, more than twice that of bass and crappies. They ate fewer prey contributing at least 5% of the diet. Shannon-Weaver diversity indices, consequently, were lower for bluegills than for bass and crappies (Table 35). Bluegills evidently "sampled" many kinds of food, but concentrated on eating a smaller variety of prey. Bass fed more evenly over the food spectrum.

The diets of small bass and bluegills overlapped by 70% (Table 36). They both occupied the littoral region and fed on *Daphnia* (37% bass, 42% bluegills) and chironomids (20% bass, 41% bluegills). The diets of medium bluegills and crappies overlapped by 90%, as both species shared *Daphnia* (90% bluegills, 84% crappies) and *Leptodora* (8% bluegills, 9% crappies). Interspecific competition may have intensified in July when *Daphnia* collapsed, forcing bluegills inshore to consume other prey. The diets ultimately diverged, since the food of all large fishes overlapped by one-fourth or less.

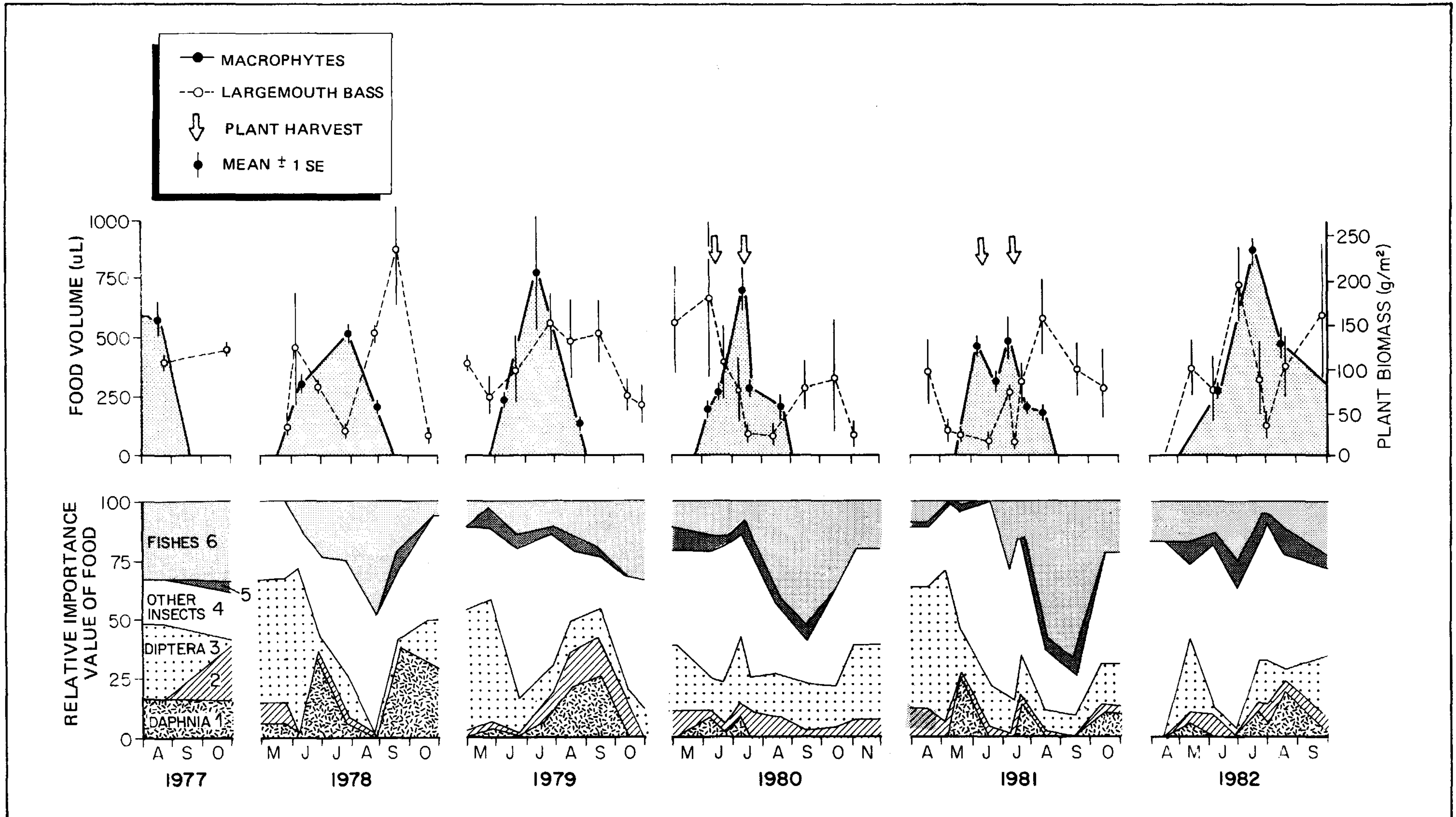

FIGURE 32. *Bass diet compared to macrophyte biomass. Smallest prey are ranked at the bottom. Prey category 5 represents mostly oligochaetes and some crayfish.*

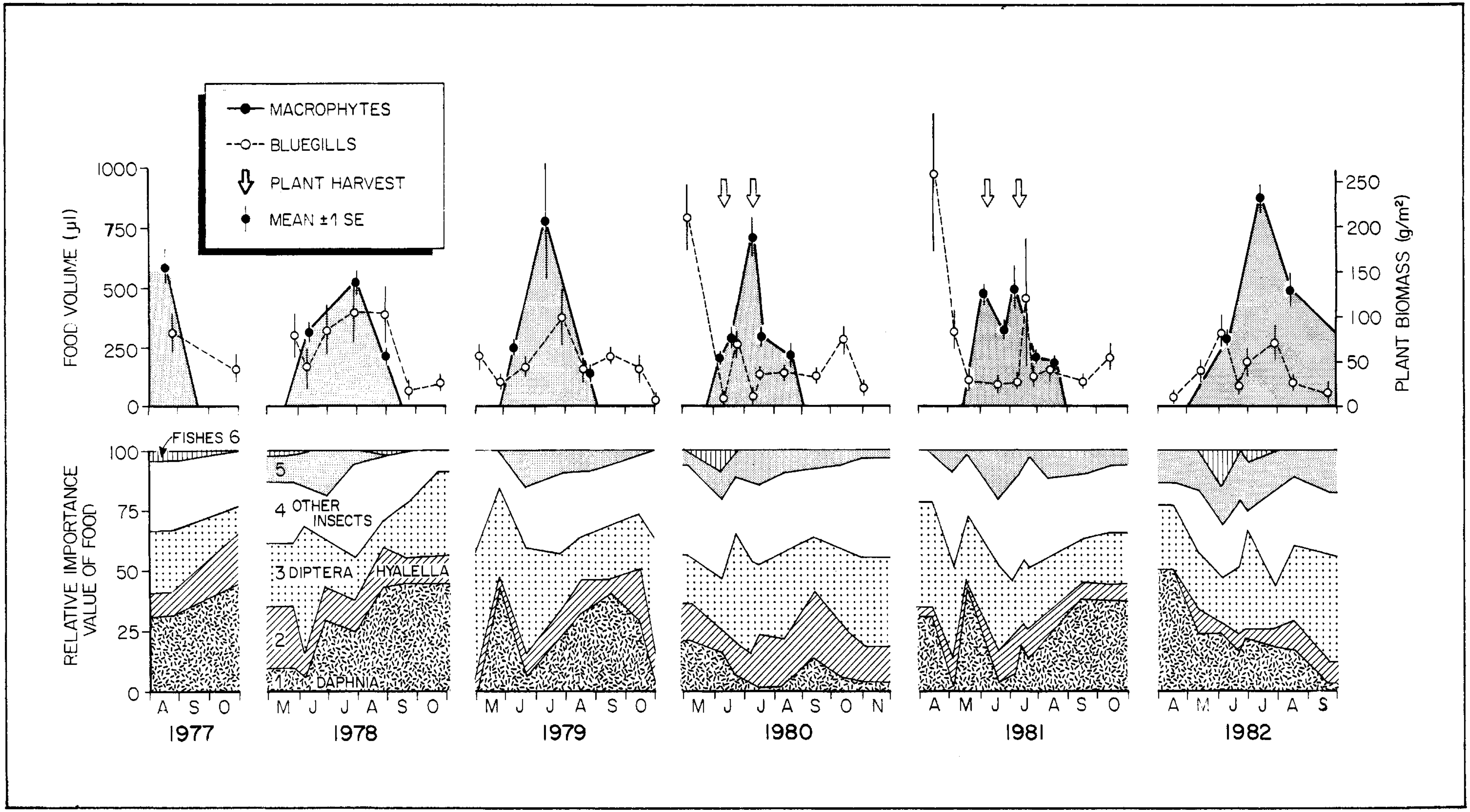

FIGURE 33. *Bluegill diet compared to macrophyte biomass. Prey category 5 includes mostly snails, oligochaetes, and water mites.*

TABLE 31. *Relative abundance of prey consumed by at least 5% of fishes of three sizes in mid-May through August 1977-79.*

Food Category	Bass			Bluegill			Crappie		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Crustacea	21	3	7	18	45	28	79	86	37
Amphipoda	3	0	0	1	1	tr	1	tr	6
Cladocera	16	2	4	12	44	27	32	39	23
Copepoda	1	tr	3	1	tr	tr	35	45	6
Ostracoda	tr[a]	1	0	3	tr	1	16	1	2
Acari	1	1	0	1	tr	9	0	0	tr
Gastropoda	0	1	0	2	3	12	0	0	tr
Insecta	65	59	46	79	49	56	11	20	55
Ephemeroptera	12	18	7	6	4	4	1	tr	1
Caenis	4	6	5	6	4	2	tr	tr	1
Callibaetis	7	10	1	tr	1	tr	1	tr	tr
Odonata	11	21	13	2	4	4	tr	tr	0
Anisoptera	3	17	8	tr	2	2	tr	0	0
Zygoptera	5	4	3	1	1	2	tr	tr	0
Hemiptera	3	13	7	tr	tr	tr	tr	tr	0
Gerris	0	9	6	tr	0	0	0	0	0
Trichoptera	0	tr	4	3	3	1	tr	tr	tr
Coleoptera	tr	0	tr	2	4	tr	0	tr	1
Diptera	37	11	15	67	35	46	10	20	52
Chaoboridae	7	1	3	1	1	14	8	3	tr
Chironomidae	26	10	11	62	32	30	2	14	51
Fish (flesh, scales)	14	35	43	tr	0	2	tr	tr	0

[a] tr = less than 0.5% of total items consumed.

TABLE 32. *Relative abundance of prey comprising at least 5% of the crappie diet for mid-May through August 1977-79, grouped by size class of prey.*

Food Category: Size (mm)	Taxon	Fish Length (mm): Under 120	120-179	Over 179
Under 1	*Bosmina*	33	tr[a]	0
	Cypria	8	1	tr
1-2	*Eucyclops*	5	0	0
	Mesocyclops	21	1	0
	Daphnia	21	84	21
5-10	*Chaoborus*	2	1	7
	Leptodora	6	9	59
Over 10	Chironomidae	1	1	16

[a] tr = less than 0.5% of diet.

TABLE 33. *Electivity indices (mean ± 1 SE) of microcrustaceans consumed by crappies on 8 dates from mid-May through August 1977-79.*

Crustacea: Size (mm)	Taxon	Fish Length (mm): Under 120	120-179	Over 179
Partial avoidance				
Under 1	*Chydorus*	-0.5 ± 0.4	-1.0 ± 0	-1.0 ± 0
	Bosmina	0.1 ± 0.3	-0.8 ± 0,2	-0.8 ± 0.2
	Cypria	-0.2 ± 0.3	-0.9 ± 0.02	-0.9 ± 0.1
1-2	*Mesocyclops*	0.01 ± 0.2	-0.8 ± 0.1	-1.0 ± 0
	Diacyclops	-0.4 ± 0.4	-0.5 ± 0.3	-1.0 ± 0
No selection				
	Eucyclops	0.4 ± 0.2	-0.2 ± 0.2	-0.2 ± 0.2
	Skistodiaptomus	0.2 ± 0.2	0.2 ± 0.2	-0.2 ± 0.2
	Daphnia	-0.3 ± 0.2	0.3 ± 0.1	-0.4 ± 0.2
	Simocephalus	-0.2 ± 0.2	0.2 ± 0.2	-0.4 ± 0.2
5-10	*Leptodora*	0.4 ± 0.2	0.2 ± 0.5	0.2 ± 0.4
No. stomachs examined		16	12	7

TABLE 34. *Number of total taxa and taxa contributing at least 5% of prey consumed by fishes of three sizes from mid-May through August 1977-79.*

Fish Length (mm)	Bass: Total	Bass: 5%	Bluegill: Total	Bluegill: 5%	Crappie: Total	Crappie: 5%
Under 120	23	3	53	2	21	6
120-179	23	4	38	3	18	2
Over 179	20	5	23	1	12	4

TABLE 35. *Shannon-Weaver diversity index (log_2) of all taxa consumed by fishes of three size ranges from mid-May through August 1977-79.*

Fish Length (mm)	Bass	Bluegill	Crappie
Under 120	3.1	2.0	2.6
120-179	2.5	1.1	1.0
Over 179	2.9	0.7	1.8

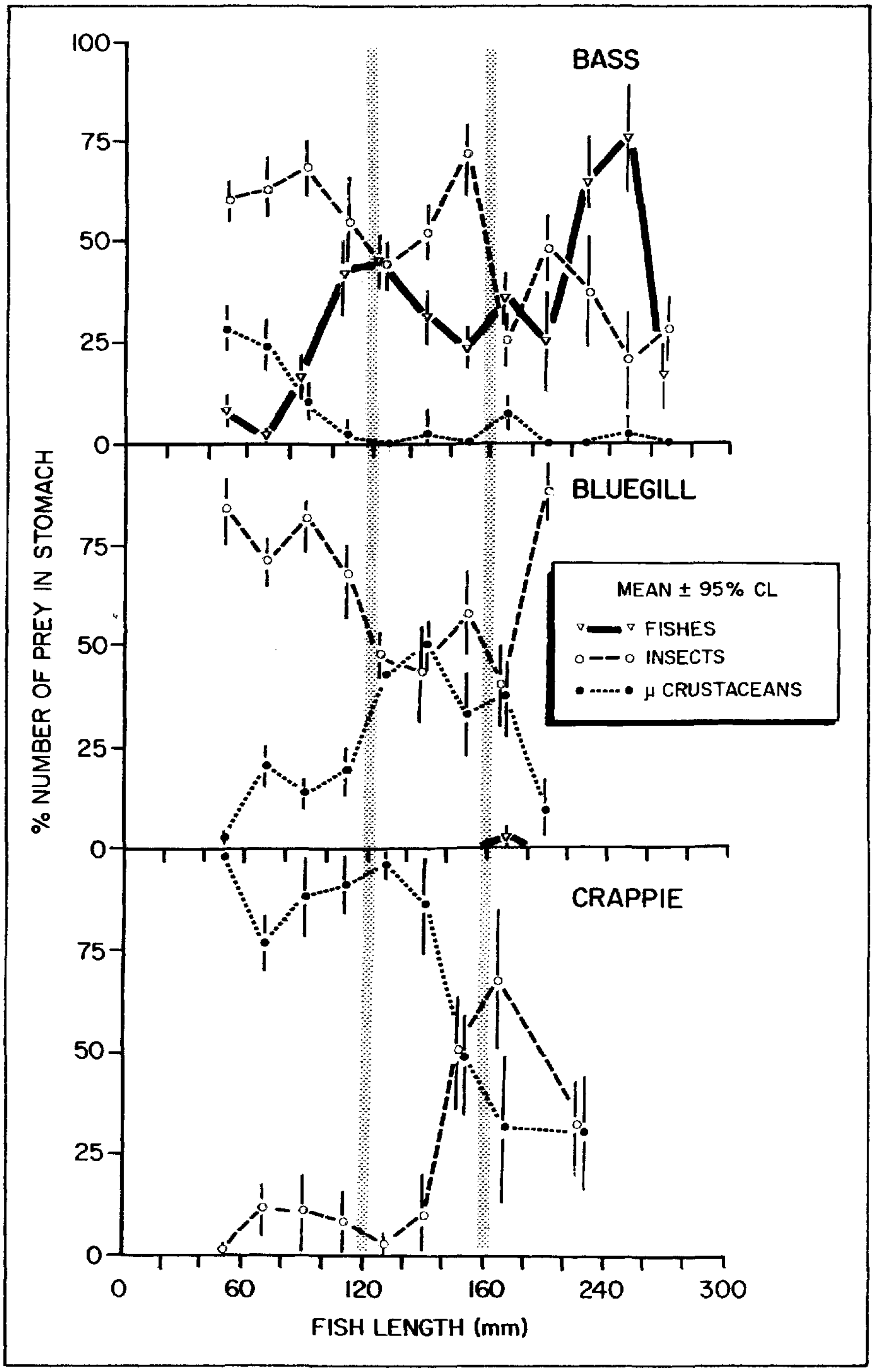

FIGURE 34. *Consumption of microcrustaceans (cladocerans, copepods, and ostracods), insects, and fry by size of predator during mid-May through August 1977-79.*

Macrophytes as Food

Nearly 20% of all bass and bluegill stomachs contained vegetation (Table 26). They held plants on about 75% of all sampling dates. Plants appeared 4-5 times as often in stomachs of large fishes as those of small ones (Table 37). Only 6% of crappie stomachs, on 15% of sampling dates, had plant matter. This reflected a greater use of zooplankton in the pelagic region.

The percent occurrence of plant matter seasonally increased for bass and bluegills, from 4-6% in April to 28-32% in September (Fig. 35). Crappie stomachs only held plants in May and August.

Bass and crappies ingested traces of vegetation. Bluegills consumed 20% by volume of their diet in plants during July and August. Some bluegill stomachs contained only vegetation; 40% had over one-tenth of their food volume in plants.

Bluegills mostly ingested leaves and young stems. Flowers, older stems, and roots were not found in stomachs. Berchtold's pondweed, elodea, and water stargrass appeared most often. Vascular plants occurred 5 times as often in stomachs as did filamentous algae. Some stomachs in July had masses of fresh green leaves, suggesting intentional browsing on macrophytes. Many stomachs in September contained plant parts and mineral detritus, reflecting accidental ingestion while grazing on benthic macroinvertebrates.

Over two dozen studies list vegetation in the bluegill diet (Table 38). Mean percent volume was typically 20-30%, but ranged from 0% to 86%. Bluegills in these studies ingested bushy pondweed, chara, coontail, duckweeds (*Lemna*, *Spirodella*, and *Wolffia*), filamentous algae, hydrilla (*Hydrilla verticillata* Royle), pondweeds, unidentified seeds, water hyacinth (*Eichornia crassipes* (Mart.)), and wild celery. Fishes were usually over age 0, with ingestion of vegetation increasing in older or larger fish (Bennett et al. 1940, Bennett 1948, Doxtater 1964, Applegate et al. 1966).

TABLE 36. *Percent overlap (Schoener 1970) of prey consumed by fishes of three sizes from mid-May through August 1977-79.*

Fish Length (mm)	Bass-Bluegill	Bass-Crappie	Bluegill-Crappie
Under 120	70	29	28
120-179	24	27	90
Over 179	11	25	25

TABLE 37. *Percent occurrence of plant matter ingested by fishes of three sizes on 44 dates in 1977-82.*

Fish Length (mm)	Bass	Bluegill	Crappie
Under 120	7	10	4
120-179	13	36	5
Over 179	34	41	20
No. fish	731	751	195

TABLE 38. *Plant matter reported in bluegill stomachs (mostly above age 0) in summer (mean percent volume and percent occurrence).*

Volume	Occurrence	Study Site	Reference
3	—	Lake Opinicon, Ontario	Keast (1978)
4	15	Unspecified waters, AL	Howell et al. (1941)
10	—	Lake Pepin, WI	Pearse (1921*a*)
—	10	Tuckahoe Creek, VA	Flemer and Woolcott (1966)
21	24	Halverson Lake, WI	Engel (present study)
0-23	—	Bull Shoals Reserv., AR-MO	Applegate et al. (1966)
23	—	Green Lake, WI	Pearse (1921*b*)
25	—	Unspecified lakes, WI	O'Donnell (1940)
27	34	Buckeye Lake, OH	Morgan (1951)
0-28	0-23,50	Lake George, FL	Huish (1957), Chable (1947 *in* Huish)
30,34	—	Muskellunge Lake, WI	Couey (1935)
35	—	Wyland Lake, IN	Gerking (1962)
26,36	—	Third Sister Lake, MI	Ball (1948)
0-39	0-61	Action Lake, OH	Doxtater (1964)
50	100	Douglas Lake, MI	Reighard (1913)
40,52	27, ≥50	Reelfoot Lake, TN	Rice (1941), McCormick (1940)
0-53	—	Winona Lake, IN	Parks (1949)
0-55	22-29	Fork Lake, IL	Bennett et al. (1940), Bennett (1948)
7-64	—	Maple Lake, MN	Seaburg and Moyle (1964)
tr-78	—	Grove Lake, MN	Seaburg and Moyle (1964)
45-79	—	Linwood Lake, MN	Lux and Smith (1960)
0-9,86	—	Lake Mendota and Yahara R., WI	Pearse (1918, 1921*b*)
—	17-78	First and Second Sister Lakes, MI	Sadzikowski and Wallace (1976)
—	83	Lake Geneva, WI	Nelson and Hasler (1942)

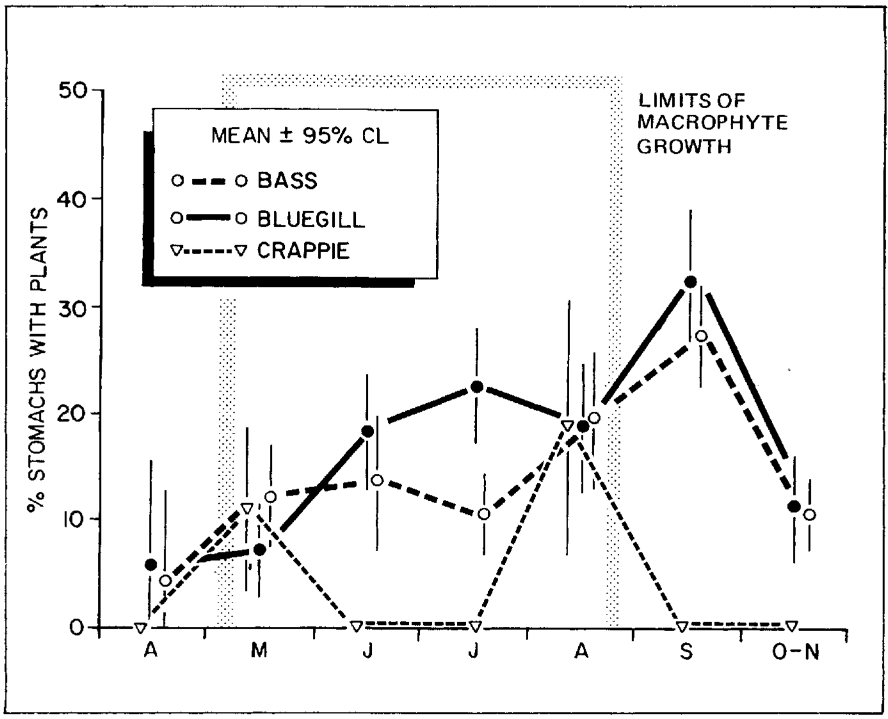

FIGURE 35. *Mean percent occurrence by month of plant matter in fish stomachs, based on 44 sampling dates in 1977-82.*

Most vegetation was consumed in June, July, or August (Ball 1948, Parks 1949, Lux and Smith 1960, Seaburg and Moyle 1964). The frequent citation of such a variety of plants, usually comprising over 20% by volume of the diet in summer, suggests that vegetation can be a major food of bluegills.

Failure to report vegetation in the bluegill diet may reflect a dearth of plants in the lakes (Couey 1935), the young age of fish sampled (Werner 1969), or abundance of more preferred macroinvertebrate prey (Howell et al. 1941). Some investigators noted considerable plant matter in the diet of bluegills, but failed to list it as a food (Roszman 1935, Etnier 1971).

Some researchers have concluded that bluegills intentionally ingest plant matter (Forbes and Richardson 1920, Bennett et al. 1940, Ball 1948, Lux and Smith 1960, Gerking 1962, Seaburg and Moyle 1964). Consumption of plants and insect larvae can be inversely proportional, suggesting that plants are an animal food substitute (Ball 1948, Parks 1949, Morgan 1951, Huish 1957). This may occur when crowding of bluegills leads to depletion of preferred animal foods (Howell et al. 1941). Bluegills may ingest plant matter as "stuffing" (Bennett et al. 1940) or "roughage" (Gerking 1962) to help masticate exoskeletons.

Bluegills may derive nourishment from plant matter, despite the absence of cellulose enzymes in the gut (Cowey and Sargent 1979). Bluegills grew best in aquaria when their diet of mealworm larvae (*Tenebrio*) and earthworms (*Lumbricus*) was supplemented with dried chara (Kitchell and Windell 1970).

Browsing on macrophytes in Halverson Lake may have been necessary when emergence of chironomid larvae in spring and depletion of *Daphnia* in early summer dwindled animal food resources. Appearance of multitudes of fry inshore in midsummer, some just hatching and others returning from offshore, may have further taxed prey resources. Switching of larger bluegills to plants may serve to reduce intraspecific competition with minimal habitat segregation.

Age and Growth

Most fishes resumed growth after mid-May. New annuli appeared on scales as early as April 24, but less than 3% of fishes displayed a new annulus by May 15. Annuli were typically completed during May 20-27, in agreement with numerous studies of these species for waters at 42° N latitude (Sprugel 1953, Carlander 1977).

Fish and macrophyte growth coincided. Fishes grew fastest in June, completing two-thirds of their annual growth by mid-July. Growth then slowed and was not appreciable after mid-September.

Fishes grew most rapidly during the first two summers of life. Bass reached 173 ± 4 mm (mean ± 95% CL) at the end of their second year (age I). They were then twice the mean length of bluegills and one-fifth that of crappies of age I (Table 39). These bass averaged 5 times the weight of bluegills and nearly twice that of crappies (Table 40).

Growth slowed for bluegills and crappies after their third summer (age II), with few fishes captured over 300 mm or age V (Fig. 36). Bass grew slower after their second summer, with few older ones caught inshore until macrophytes decayed. Older fishes often resided in water too deep for electrofishing, judging from angling.

Bass grew slower, bluegills about average, and crappies faster in Halverson Lake than in 10 studies of 300 waters from Iowa, Michigan, Minnesota, and Wisconsin (Fig. 37). Bluegill growth varied among waters, but bass grew slower in waters of dense vegetation, suggesting difficulty in gaining access to forage fishes. Bluegill growth in Halverson Lake was similar to that in many lakes outside the Midwest (Serns and Strawn 1975, Carlander 1977).

TABLE 39. *Changes in mean length with age, measured at the time of capture, for fishes randomly selected from electrofishing catches in August or October 1977-82.*[a]

	Total Length (mm) by Age Group						
Parameter	0	I	II	III	IV	V	>V
Bass							
Mean	88	173	223	258	281	292	449
± 95% CL	3	4	5	9	17	8	35
No.	159	102	66	37	19	11	11
Bluegill							
Mean	—	89	136	164	186	200	226
± 95% CL	—	2	2	3	5	12	32
No.	—	192	146	77	33	11	3
Crappie							
Mean	78	142	212	239	252	266	—
± 95% CL	5	5	22	114	0	28	—
No.	45	53	3	2	1	3	—

[a] Based on measurements of unpreserved, unmarked fishes.

TABLE 40. *Changes in mean fresh weight of fishes randomly selected from electrofishing catches in August or October 1977-82.*

	Body Weight (g) by Age Group						
Parameter	0	I	II	III	IV	V	>V
Bass							
Mean	9	70	149	242	311	336	1629
± 95% CL	1	5	12	30	65	28	519
No.	153	102	66	37	19	11	10
Bluegill							
Mean	—	14	50	84	131	178	252
± 95% CL	—	1	3	6	14	31	115
No.	—	190	146	77	33	11	3
Crappie							
Mean	6	39	134	227	268	270	—
± 95% CL	2	4	77	13	0	24	—
No.	42	53	3	2	1	3	—

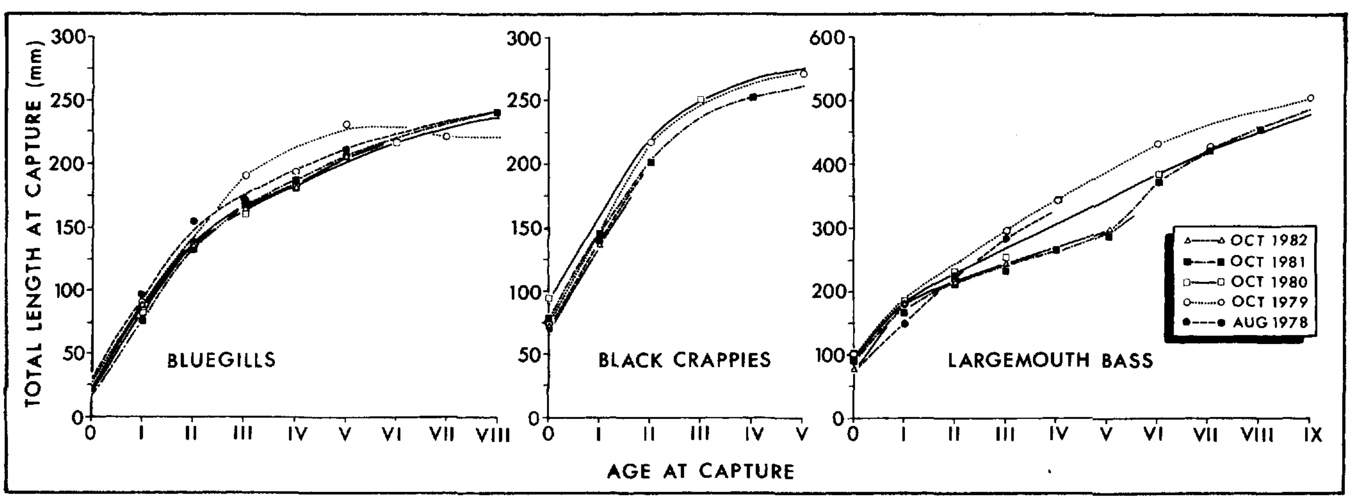

FIGURE 36. *Mean length of fishes by scale age for August or October of each sampling year.*

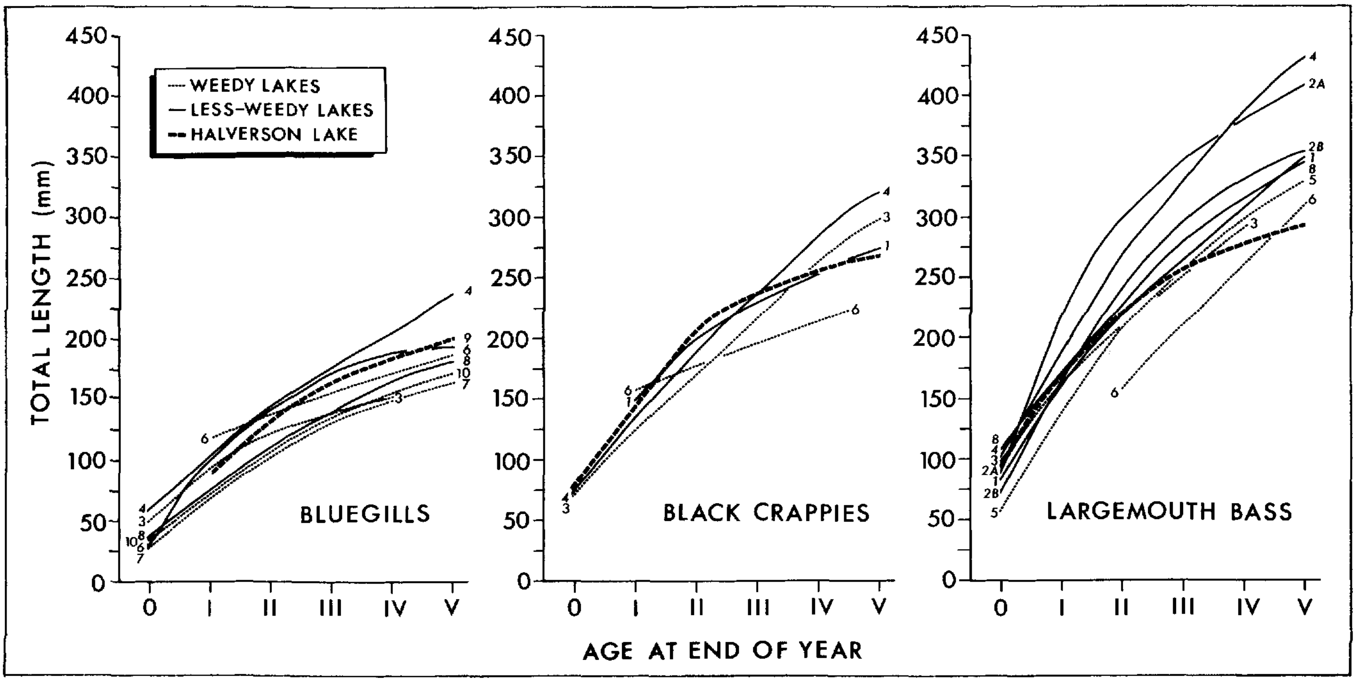

FIGURE 37. *Mean length by age of fishes from Halverson Lake and waters in Wisconsin and neighboring states. These are identified by number as 1 (Beckman 1946: 175 Michigan lakes); 2 (Bennett 1937: A-18 lakes and B-Yahara River chain, southern Wisconsin); 3 (Churchill 1976: Lake Wingra, southern Wisconsin in 1972-74); 4 (Eddy and Carlander 1942: 79 Minnesota lakes); 5 (Kmiotek and Cline 1952: 13 southern Wisconsin lakes); 6 (Mackenthun 1946: 17 southern Wisconsin lakes); 7 (Mayhew 1956: West Okoboji Lake, Iowa); 8 (Parker 1958: Flora Lake, northern Wisconsin); 9 (Schloemer 1939: Lake Wingra in 1936); and 10 (Snow 1969: Murphy Flowage, northern Wisconsin).*

Length-Weight Relations

The relationship of length to weight in fish populations was curvilinear, until transformed by common logarithms (Fig. 38). Fishes grew faster in weight than in length, as suggested by annual regression slopes above 3.0 for all species (Table 41). The slopes averaged 3.19 ± 0.06 for bass, 3.41 ± 0.07 for bluegills, and 3.68 ± 0.16 for crappies. The population of slow-growing bluegills in Lake Wingra, Wisconsin had a regression slope of 3.06 in 1972-74 (Churchill 1976). Slopes for bluegills and crappies were above average, but average for bass, compared with numerous populations cited by Carlander (1977).

Mean condition factor (K) was higher for bluegills than for bass and changed seasonally in both species (Fig. 39). It peaked in June and July for bluegills (1.9-2.2), when macrophytes were densest, and in June for bass (1.3-1.5). Such condition factors indicate average plumpness in Illinois populations (Bennett 1948). Condition declined in late summer or fall for bluegills (1.5-1.7) and bass (1.0-1.3). It was often low in early spring, suggesting reduced condition during winter.

Fish condition changed with age. Mean condition factor for bluegills increased 17% from age I (1.63) to age IV (Fig. 40). An increase with age was also suggested for crappies, but low sample sizes of older fish precluded further comparisons. Drop in mean condition factor of bluegills after July partly resulted from catching a higher proportion of age 0 fishes.

Standing Crop

The number of fishes over 49 mm fluctuated widely among years (Fig. 41). Bluegills this size were 3-5 times as numerous as bass in most years. Bluegill numbers averaged 2,100 ± 60 for October 1978-82, compared to 620 ± 135 for bass. Sample sizes were too low to adequately estimate numbers of crappies.

Annual biomass of fishes over 49 mm averaged 46 ± 11 kg/ha for bluegills and 16 ± 3 kg/ha for bass, but varied widely among years (Table 42). It fluctuated 3-fold for bass (9-27 kg/ha) and 6-fold for bluegills (12-74 kg/ha). Swingle (1950) also found bluegills to average 3 times the biomass of bass of all sizes, when 26 "balanced" lakes or ponds in Alabama were drained or poisoned.

Variations in fish standing crop appeared unrelated to macrophyte biomass, despite such claim in Clear Lake, Iowa (DiCostanzo 1957). The population size of bluegills varied between years both before and during years of plant harvesting. Centrarchid populations are often unstable in the same basin (Regier 1963) and usually cannot be simply related to changes in other biotic communities.

INTERACTIONS WITH PLANKTON

Composition

Cladocerans, copepods, and rotifers comprised over 80% of the 72 species of zooplankton netted in the pelagic region (Fig. 42). Green algae and desmids, diatoms and blue-green algae contributed over 80% of the 114 species of phytoplankton found offshore. Rotifers accounted for over 50% of all zooplankton species; green algae made up nearly 40% of all phytoplankton. Fewer species of plankton were found, however, than macroinvertebrates (Table 11).

Many plankton were typical of ponds and shallow fertile lakes (Tables 43 and 44). They occurred on or beneath submerged macrophytes, where some were grazed by chironomid larvae (Table 23), and rarely became abundant offshore. Such **meroplankton**

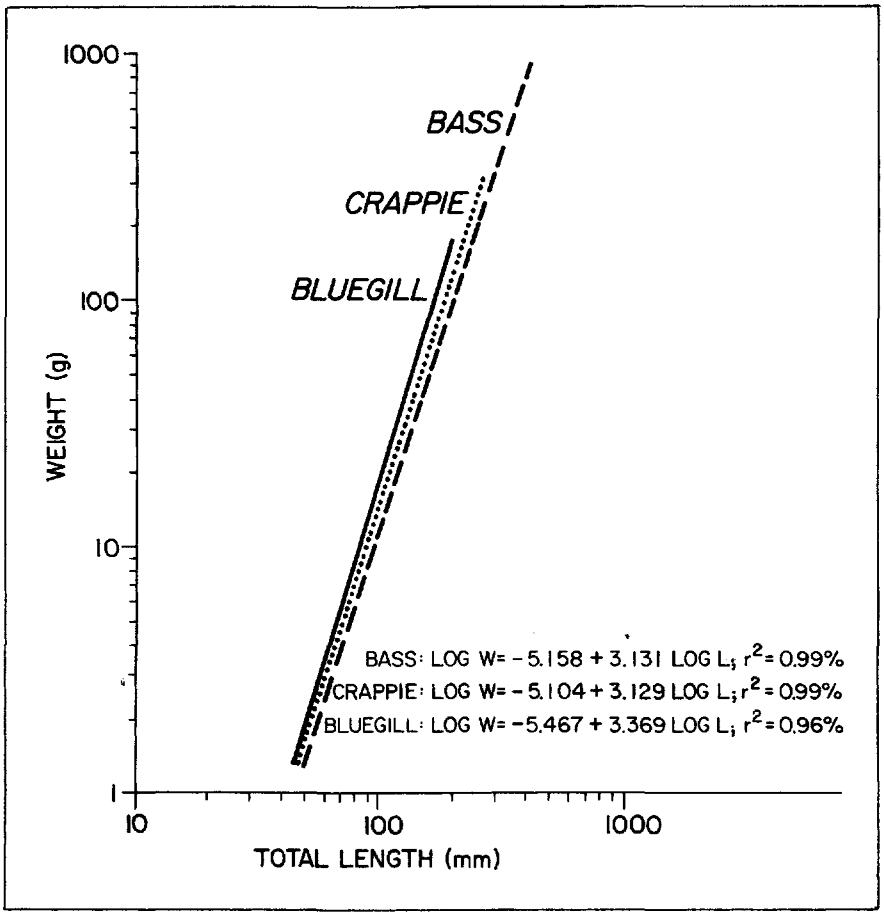

FIGURE 38. *Log length-log weight regressions of fishes for August 1977-79.*

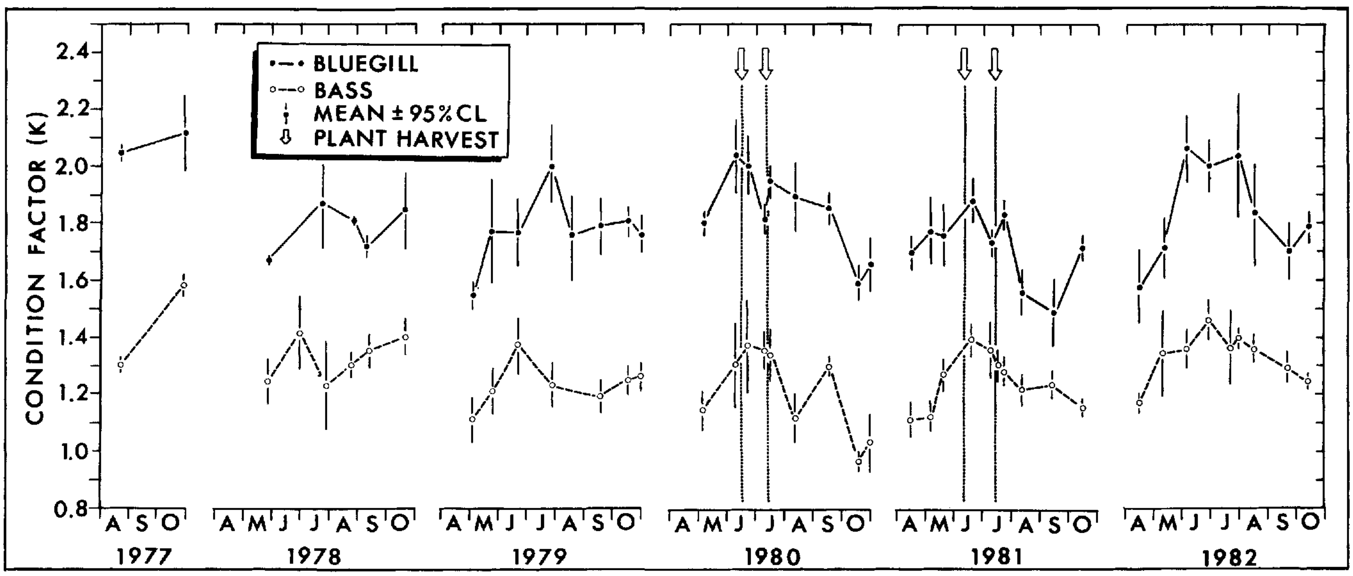

FIGURE 39. *Seasonal changes in mean condition factor for samples of 5 or more fish in 1977-82.*

TABLE 41. *Log length-log weight regression slopes (b) of fishes.*

Sampling Date	Regression Slope (no. fish)					
	Bass		Bluegill		Crappie	
1977 Aug	3.03	(350)	3.13	(331)	3.06	(10)
1978 Aug	3.19	(45)	3.48	(304)	3.21	(8)
1979 Oct	3.18	(100)	3.37	(178)	3.19	(11)
1980 Oct	3.46	(301)	3.55	(268)	3.92	(23)
1981 Oct	3.22	(162)	3.57	(289)	3.94	(73)
1982 Oct	3.05	(177)	3.34	(154)	3.36	(29)

TABLE 42. *Standing crop (kg/ha ± 95% CL) of bass and bluegills over 49 mm in August or October 1977-82.*

Year	Bass	Bluegill
1977	18 ± 16	—
1978	18 ± 15	60 ± 61
1979	27 ± 84	75 ± 65
1980	9 ± 16	52 ± 62
1981	12 ± 26	32 ± 54
1982	10 ± 26	12 ± 15

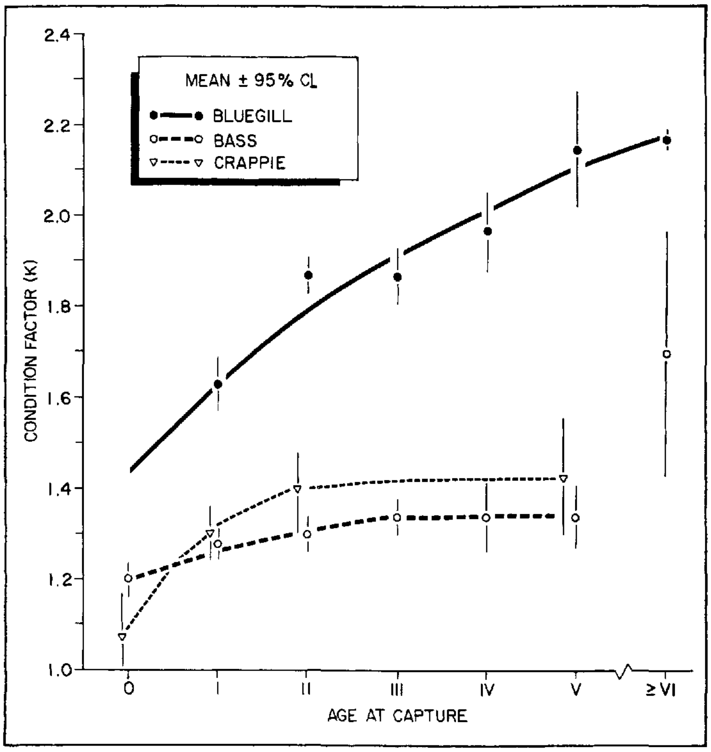

FIGURE 40. *Mean condition factor by scale age for fish samples pooled for August or October 1977-82.*

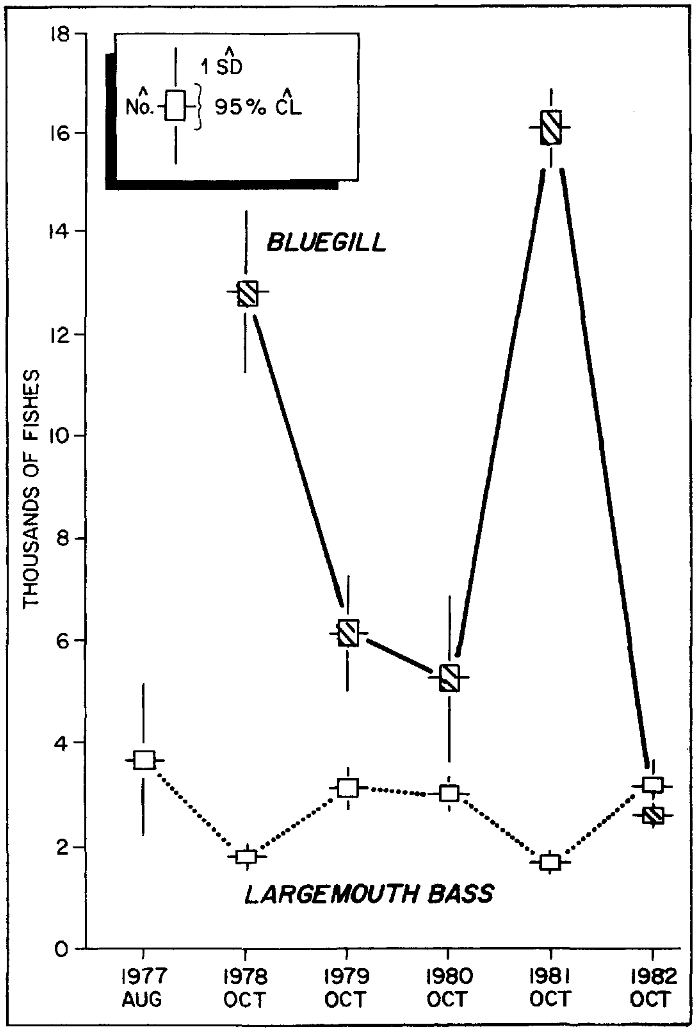

FIGURE 41. *Estimated number of bass and bluegills over 49 mm sampled each August or October, using the Bailey-modified Petersen formula (Ricker 1975).*

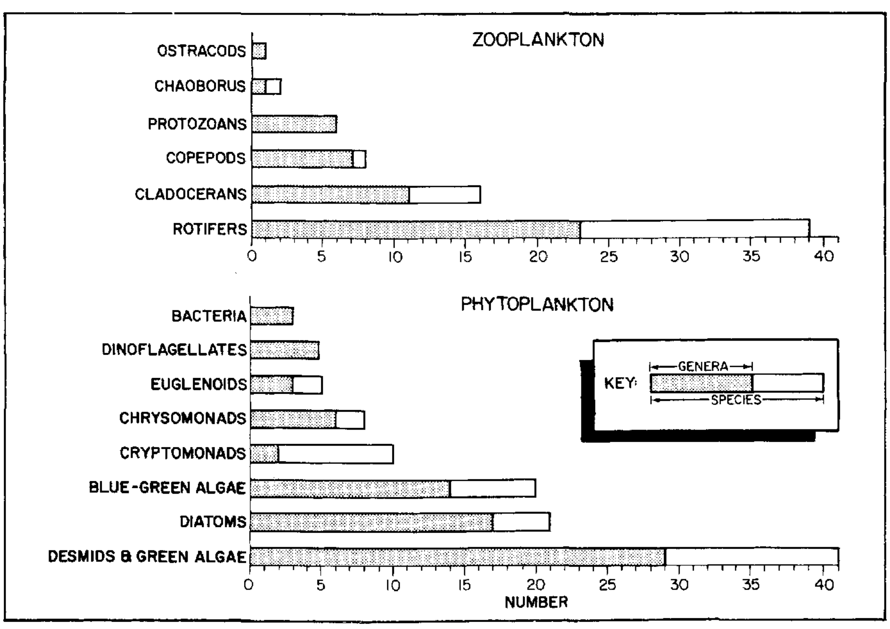

FIGURE 42. *Number of genera (shaded bars) and species (complete bars) distributed among the major groups of phytoplankton and net zooplankton collected at Stations B or C in 1977-82.*

TABLE 43. *Zooplankton netted in 1977-82 at Stations B and C.*[a]

Protozoa

Acanthocystis sp.
Difflugia urceolata Carter
Euglena sp.
Phacas longicauda (Ehrenberg)
Trichodina sp.
Vorticella sp.

Rotifera

Ascomorpha ecaudis Perty
A. (Chromogaster) ovalis (Bergendal)
A. saltans Bartsch
Asplanchna brightwelli Gosse
A. priodonta Gosse
Cephalodella gibba (Ehrenberg)
Collotheca mutabilis (Hudson)
C. pelagica (Rousselet)
Conchiloides dossuarius (Hudson)
C. natans (Seligo)
Conchilus unicornis Rousselet
Euchlanis triquetra Ehrenberg
Filinia longiseta (Ehrenberg)
Gastropus hyptopus (Ehrenberg)
G. stylifer Imhof
Keratella c. cochlearis (Gosse)
K. c. var. *hispida* (Lauterborn)
K. c. f. *micracantha* (Lauterborn)
K. c. f. *tecta* (Lauterborn)
Lecane clara (Bryce)
L. inopinata Harring and Myers
Lepadella ovalis (Müller)
Monostyla lunaris (Ehrenberg)
M. quadrindentata Ehrenberg
Mytilina ventralis (Ehrenberg)
Notholca acuminata (Ehrenberg)
N. a. var. *extensa* Olofsson
Platyias patulus (Müller)
P. quadricornis (Ehrenberg)
Polyarthra dolichoptera Idelson
P. euryptera Wierzejski
P. vulgaris Carlin
Pompholyx sulcata Hudson
Synchaeta oblonga Ehrenberg
S. pectinata Ehrenberg
Testudinella patina f. *triloba* (Herman)
Trichocerca cylindrica (Imhof)
T. longiseta (Shrank)
T. multicrinis (Kellicott)
T. rouseletti (Voigt)
T. similis (Wierzejski)
Trichotria pocillum (Müller)
T. tetractis (Ehrenberg)

Insecta: Diptera

Chaoborus albatus Johnson
C. punctipennis (Say)

Cladocera

Alona circumfimbriata Megard
Bosmina longirostris (Müller)
Ceriodaphnia reticulata (Jurine)
Chydorus sphaericus (Müller) sens. lat.
Daphnia ambigua Scourfield
D. galeata Sars *mendotae* Birge
D. parvula Fordyce
D. retrocurva S. A. Forbes
Diaphanosoma brachyurum (Liéven)
[= *D. leuchtenbergianum* Fischer]
Eurycercus longirostris Hann
[= *E. lamellatus* (Müller) sens. lat.]
Leptodora kindtii (Focke)
Leydigia leydigii (Schødler)
[= *L. quadrangularis* (Leydig)]
Pleuroxis denticulatus Birge
P. hastatus Sars
Simocephalus serrulatus (Koch)
S. vetulus Schodler

Copepoda: Calanoida

Skistodiaptomus pallidus (Herrick)

Copepoda: Cyclopoida

Acanthocyclops vernalis (Fischer)
Diacyclops thomasi (S. A. Forbes)
[= *C. bicuspidatus thomasi* (Forbes)]
Eucyclops serrulatus (Fischer)
[= *E. agilis* (Koch)]
E. speratus (Lilljeborg)
Macrocyclops albidus (Jurine)
Mesocyclops edax (S. A. Forbes)
Tropocyclops prasinus (Fischer)

Ostracoda

Cypria ophthalmica (Jurine)

[a] Rotifers were identified from Voigt (1956), Gilbert et al. (1979), and especially Stemberger (1979); cladocerans from Megard (1967) for *Alona*, Deevey and Deevey (1971) and Kořinek (1971) for *Bosmina*, Brandlova et al. (1972) for *Ceriodaphnia*, Brooks (1957) for *Daphnia*, Kořinek (personal identification) for *Diaphanosoma*, and Edmondson (1959) for other species; copepods from Torke (1975 unpubl. rep., 1976) and Smith and Fernando (1978); ostracods from Nuttall and Fernando (1971); and *Chaoborus* from Cook (1956). Nomenclature for *Eurycercus* followed Hann (1980).

included protozoans (*Euglena, Phacus,* and *Vorticella*), rotifers (*Euchlanis, Monostyla, Mytilina,* and *Platyias*), and microcrustaceans (*Alona, Ceriodaphnia, Cypria, Eurycercus, Leydigia, Macrocyclops, Pleuroxis,* and *Simocephalus*). Also common inshore were green algae (*Ankistrodesmus, Cosmarium, Gloeocystis, Pleodorina, Scenedesmus,* and *Volvox*), diatoms (*Melosira, Navicula, Pinnularia,* and *Synedra*), and a blue-green alga (*Gloeotrichia*).

The most abundant species in Halverson Lake were common to pelagic regions of lakes. *Ascomorpha, Daphnia, Diacyclops, Keratella, Mesocyclops, Polyarthra,* and *Skistodiaptomus* accounted for 80% of all zooplankton collected in six years. *Anabaena, Ceratium, Cryptomonas, Erkenia, Microcystis,* and *Ochromonas* produced 50% of all algal cells and 70% of the total biovolume in pelagic samples.

Such diverse pelagic assemblages, mixing true plankton with partly littoral and benthic species, reflects the small area and shallow depth of the lake, its broad littoral region, and support of microfauna and their food by submerged macrophytes.

Few species were found on any date. For all dates zooplankton samples averaged 14 ± 0.3 species; phytoplankton samples had 16 ± 1.1 species. Most species were rare. Although 40% of all species recurred in at least 5% of samples, only 5-10% of them contributed over 5% of the total abundance (Table 45).

One-half of all phytoplankton species exceeded 35 μm, a size considered too large for most zooplankton to consume (Watson and Kalff 1981). These net plankton were mainly multicellular green and blue-green algae, but also included chrysomonads, large diatoms, big dinoflagellates (*Ceratium*), and euglenoids (Table 44). Edible-sized phytoplankton consisted of 39 genera and 53 species of **nannoplankton.** They

TABLE 44. ***Cell size (greatest dimension) and biovolume of phytoplankton (mean ± 1 SE) identified from Kemmerer samples in 1977-82 at Station C.***[a]

Taxon	Cell size (µm)	Biovolume (μm^3)	Sample Size
Chlorophyta: Chlorophyceae (desmids and green algae)			
Ankistrodesmus falcatus var. *acicularis* (Braun) West	—	—	0
A. f. var. *mirabilis* (West & West) G. S. West	58 ± 18	40 ± 0	2
Arthrodesmus sp.	10	410	1
Carteria sp.	9 ± 0.8	250 ± 110	7
Chlamydomonas spp. (2)	7 ± 0.6	250 ± 390	36
Chlorella vulgaris Beyerninck	12	905	1
Chlorococcum infusionum (Schrank) Menghini	15	115 ± 25	4
Chlorogonium sp.	—	40	1
Closterium gracile De Brébisson	—	710	1
Coelastrum microporum Nägeli	5 ± 1	70 ± 40	2
Cosmarium sp.	18 ± 4	1810 ± 410	4
Dictyosphaerium pulchellum Wood	4	30	1
Euastrum sp.	22	1380	1
Franceia ovalis (Francé) Lemmermann	—	—	0
Gloeocystis sp.	—	—	0
Golenkinia sp.	16	260	1
Kirchneriella subsolitaria G. S. West	10	75 ± 10	3
Oöcystis spp. (4)	11 ± 0.6	350 ± 120	22
Pediastrum Boryanum (Turpin) Meneghini	—	1250	1
Pleodorina californica Shaw	—	—	0
Quadrigula Chodatii (Tanner-Fullman) G. M. Smith	16	50 ± 17	2
Q. lacustris (Chodat) G. M. Smith	18 ± 3	70 ± 14	4
Scenedesmus abundans (Kirchner) Chodat	—	30	1
S. bijuga (Turpin) Lagerheim	9 ± 0.6	80 ± 26	3
S. denticulatus Lagerheim	10 ± 1.5	55 ± 13	4
S. quadricauda (Turpin) De Brébisson	10 ± 1	95 ± 20	5
Schroederia setigera (Schröder) Lemmermann	13 ± 0.9	40 ± 8	12
S. Judayi G. M. Smith	7 ± 4	40 ± 8	4
Selenastrum minutum (Nägeli) Collins	11 ± 1	60 ± 13	3
Spaerocystis Schroeteri Chodat	6 ± 0.6	120 ± 37	15
Staurastrum sp.	26 ± 4	3230 ± 840	6
Tetraëdron minimum (Braun) Hansgirg	—	230	1
T. muticum (Braun) Hansgirg	—	—	0
T. trigonum var. *gracile* (Reinsch) De Toni	—	—	0
Volvox aureus Ehrenberg	—	—	0
Chrysophyta: Chrysophyceae (chrysomonads)			
Dinobryon cylindricum Imhof	12	225	1
D. sertularia Ehrenberg	10 ± 0.5	165 ± 15	6
Erkenia subaequiciliata Skuja	3 ± 0.1	15 ± 2	26
Mallomonas caudata Iwanoff	20 ± 1.5	3420 ± 600	12
Ochromonas spp. (2)	7 ± 0.2	100 ± 40	27
Synura uvella Ehrenberg	13 ± 1	460 ± 40	3
Uroglenopsis americana (Calkins) Lemmermann	8 ± 0.2	150	2
Pyrrophyta: Cryptophyceae (cryptomonads)			
Chroomonas acuta Utermöhl	9 ± 0.2	115 ± 9	33
C. coerulea (Geitler) Skuja	7 ± 0.8	80 ± 10	14
C. reflexa Kisselew	13 ± 0.9	330 ± 24	7
Cryptomonas erosa Ehrenberg	27 ± 2	2280 ± 670	5
C. marssonii Skuja	14	590	1
C. ovata Ehrenberg	23 ± 1	1700 ± 220	9
Pyrrophyta: Dinophyceae (dinoflagellates)			
Ceratium hirundinella (Müller) Schrank	50 ± 2	50,200 ± 50,010	16
Glenodinium pulvisculus (Ehrenberg) Stein	19 ± 4	3750 ± 3010	12
Gymnodinium sp.	14 ± 0.6	845 ± 85	2
Hemidinium sp.	16 ± 0	680	2
Peridinium cinctum (Müller) Ehrenberg	59 ± 1	62,800	2
Euglenophyta: Euglenophyceae (euglenoids)			
Euglena spp. (2)	103 ± 43	23,600 ± 8050	3
Phacus sp.	26 ± 1	1340 ± 925	3
Trachelomonas sp.	15	2240 ± 1950	2
Chrysophyta: Bacillariophyceae (diatoms)			
Amphora ovalis Kützing	21 ± 9	1980 ± 1860	2
Achnanthes minutissima Kützing	4	7	1
Amphiprora sp.	—	—	0
Asterionella formosa Hassall	64 ± 11	540 ± 250	25
Cocconeis sp.	20	125	1
Cyclotella sp.	10	750 ± 43	2
Cymbella sp.	20	190	1
Fragilaria crotonensis Kitton	55 ± 7	670 ± 620	17
Melosira granulata (Ehrenberg) Ralfs	28 ± 3	760 ± 185	10
Navicula sp.	20 ± 3	470 ± 85	4
Nitzschia sp.	85	265	1
Pinnularia sp.	32	270	1
Rhopalodia sp.	65	2180	1
Stephanodiscus tenuis Ehrenberg	6	100 ± 10	9
Surirella sp.	25	1880	1
Synedra acus Kützing	69 ± 3	490 ± 95	3
S. delicatissima var. *angustissima* Grun.	190	1380	1
S. radicans Kützing	56 ±4	—	2
S. ulna (Nitzschia) Ehrenberg	186 ± 12	10,030 ±1400	4
Cyanophyta: Myxophyceae			
Anabaena planctonica Brunnthaler	10 ± 0.6	430 ± 100	13
A. spiroides Klebahn	9 ± 0.3	420 ± 75	13
Aphanizomenon flos-aquae (Linnaeus) Ralfs	7 ± 1	120 ± 55	14
Aphanocapsa (Anacystis) pulchra (Kützing) Rabenhorst	4 ± 0.4	20 ± 10	7
A. elachista West & West	2 ± 0.2	3 ± 1	3
Aphanothece sp.	5	30 ± 7	2
Coelosphaerium Kuetzingianum Nägeli	2	4	1
C. Naegelianum Unger	5 ± 0.3	20 ± 4	18
Chroococcus dispersus var. *minor* G. M. Smith	4 ± 0.5	24 ± 6	4
C. limneticus Lemmermann	—	—	0
Gloeotrichia natans (Hedwig) Rabenhorst	—	—	0
Marssoniella elegans Lemmermann	5	—	1
Merismopedia glauca (Ehrenberg) Nageli	2 ± 0.2	8 ± 2	13
Microcystis (Polycystis) aeruginosa Kützing	5 ± 0.3	55 ± 10	15
M. incerta Lemmermann	3	8	1
Oscillatoria sp.	8 ± 2	105 ± 35	2
Phormidium mucicola Naumann & Huber-Pestalozzi	2 ± 0.2	4 ± 2	5
Trichodesmium sp.	—	—	*0*
Bacteria			
Achroonema sp.	4	7	1
Chlorobium sp.	—	—	0
Thiopedia rosea Winogradsky	4	—	1

[a] Genera and species were identified from Anton and Duthie (1981) for *Cryptomonas*, Patrick and Reimer (1966, 1975) and especially Weber (1971) for diatoms, Skuja (1948) for bacteria and *Erkenia*, and Smith (1950) and especially Prescott (1962) for most other algae.

consisted chiefly of unicellular flagellates, small diatoms, and bacteria that together constituted one-half of all algal cells and biovolume. Each sample, therefore, contained an even smaller component in edible-sized species.

About 80% of all zooplankton species were less than 0.9 mm long (excluding antennae, setae, and spines) and too small for ingestion even by young centrarchids. Although these fishes mostly grazed microcrustaceans, two-thirds of their prey (14% of all net zooplankton) were still undersized. Nauplii, comprising one-half of all microcrustaceans, went ungrazed by fishes. Secondary production in the pelagic region, ultimately, remained directly underutilized by fishes.

TABLE 45. *Percent species of phytoplankton and net zooplankton contributing at least 5% of all individuals (plant cells) or samples during 1977-82.*

Contribution of Species	Species Sampled	
	Zooplankton	Phytoplankton
Total individuals or cells (%)	10	5
Total samples (%)	40	43
No. samples	68	114

TABLE 46. *Seasonal differences in zooplankton abundance (mean ± 1 SE individuals/L) for 1977-82.*

Taxon	Feb	Apr-May	Jun-Aug	Oct-Nov
Ostracods	0	2 ± <1	6 ± 1	tr[b]
Cladocerans	5 ± 1	25 ± 5	26 ± 4	5 ± 1
Calanoids[a]	9 ± 2	35 ± 9	13 ± 2	15 ± 4
Cyclopoids	49 ± 18	98 ± 17	23 ± 2	42 ± 12
Rotifers	97 ± 38	97 ± 14	77 ± 14	259 ± 69
No. samples	9 (6)	27 (18)	53 (36)	18 (10)

[a] Calanoids were calculated for just 1980-82, when they were mostly found; their sample sizes are shown in parentheses.
[b] tr = less than 0.5 individuals/L.

Seasonal Changes

Zooplankton populations fluctuated seasonally. Ostracods and cladocerans were mainly warm water forms; copepods and rotifers occurred yearlong, but usually amassed during cool weather (Fig. 43). Total abundance generally increased both in May, when cool and warm water species overlapped, and in October-November, when enormous populations of rotifers developed. Ostracods were the least abundant group and disappeared in late fall and winter; rotifers were the most numerous and populated all 72 samples (Table 46). Winter samples were sometimes abundant, but contained the lowest diversity (Table 47). These changes appeared related to water temperature.

TABLE 47. *Seasonal differences in species diversity (mean ± 1 SE) of all plankton sampled in 1977-82.*

Parameter	Feb	Apr-May	Jun-Aug	Oct-Nov
Zooplankton				
No. species	8.7 ± 0.4	12.3 ± 3.2	14.2 ± 2.4	15.7 ± 0.6
SW diversity ($\log_2$)	1.8 ± 0.2	2.4 ± 0.2	2.5 ± 0.1	2.0 ± 0.1
Percent evenness	60 ± 4	60 ± 3	66 ± 2	51 ± 3
No. samples	9	26	53	18
Phytoplankton				
No. species	8.2 ± 1.9	14.0 ± 1.0	16.4 ± 0.8	15.2 ± 1.1
SW diversity ($\log_2$)	1.7 ± 0.5	2.1 ± 0.1	2.2 ± 0.1	2.0 ± 0.2
Percent evenness	56 ± 13	56 ± 3	54 ± 3	50 ± 3
No. samples	4	14	27	10

Plankton populations varied among years. Ostracods became scarcer each succeeding summer (Fig. 43). Cladocerans developed large populations during 1980 and 1981. Calanoid copepods were rare before 1980 and then populated samples in spring and fall. Rotifers formed large populations in February 1980 and 1981, when little snow covered the lake ice (Table 5).

From mid-May through August, when submerged macrophytes were abundant, pelagic rotifers were variously dominated by *Keratella*, *Polyarthra*, *Pompholyx*, or *Trichocerca* (Fig. 44), while microcrustaceans consisted chiefly of *Daphnia*, *Diacyclops*, and *Mesocyclops* (Fig. 45). Edible-sized zooplankton contributed one-third of all individuals. *Daphnia galeata mendotae* (0.8-1.6 mm carapace length) was the sole cladoceran species in one-third of summer samples. *Mesocyclops* largely replaced *Diacyclops* after May.

Zooplankton usually declined in late summer, when *Daphnia*, *Keratella*, and nauplii populations plummeted (Figs. 44 and 45). They were partly replaced on some dates by *Filinia*, *Pompholyx*, or *Trichocerca*. *Daphnia*, however, recovered after plant harvests in 1981. These changes occurred while most submerged macrophytes senesced, blue-green algae bloomed, and water temperatures usually stayed above 20 C. The zooplankton recovered at overturn in mid-September, when populations of *Ascomorpha*, *Diacyclops*, and *Keratella* exploded.

Phytoplankton also fluctuated seasonally. Blue-green algae and occasionally bacteria (*Thiopedia*) amassed in summer; chrysomonads, cryptomonads, and diatoms bloomed in spring and fall; and green algae and dinoflagellates pulsed irregularly during ice-free periods (Figs. 46 and 47). Winter samples were usually sparse, dominated by chrysomonads and diatoms, and contained fewer species than samples in ice-free periods (Table 47).

Spring and fall blooms were variously dominated by *Asterionella*, *Erkenia*, *Fragilaria*, *Ochromonas*, *Stephanodiscus*, *Synedra*, and cryptomonids (Figs. 48 and 49). Blooms varied widely in abundance and composition among years. *Stephanodiscus* was especially abundant in 1978 and 1979, whereas *Kirchneriella* occurred abundantly on only two dates.

Blue-green algae dominated the plankton from late June or early July until fall overturn, usually contributing over 80% of all cells (Fig. 50). Maximum standing crop occurred in August, when total phytoplankton was 24,000 ± 4,000 cells/ml and 9 ± 2 mm^3/L. *Anabaena* and *Microcystis* comprised 72% by number (96% by volume) of all blue-green algae sampled. *Aphanizomenon* and *Coelosphaerium* accounted for 20% by number (4% by volume) of the algae. *Microcystis* disappeared after summer, but the other species formed a smaller bloom (4,000 cells/ml) in October or November. Blue-green algae became rare in winter.

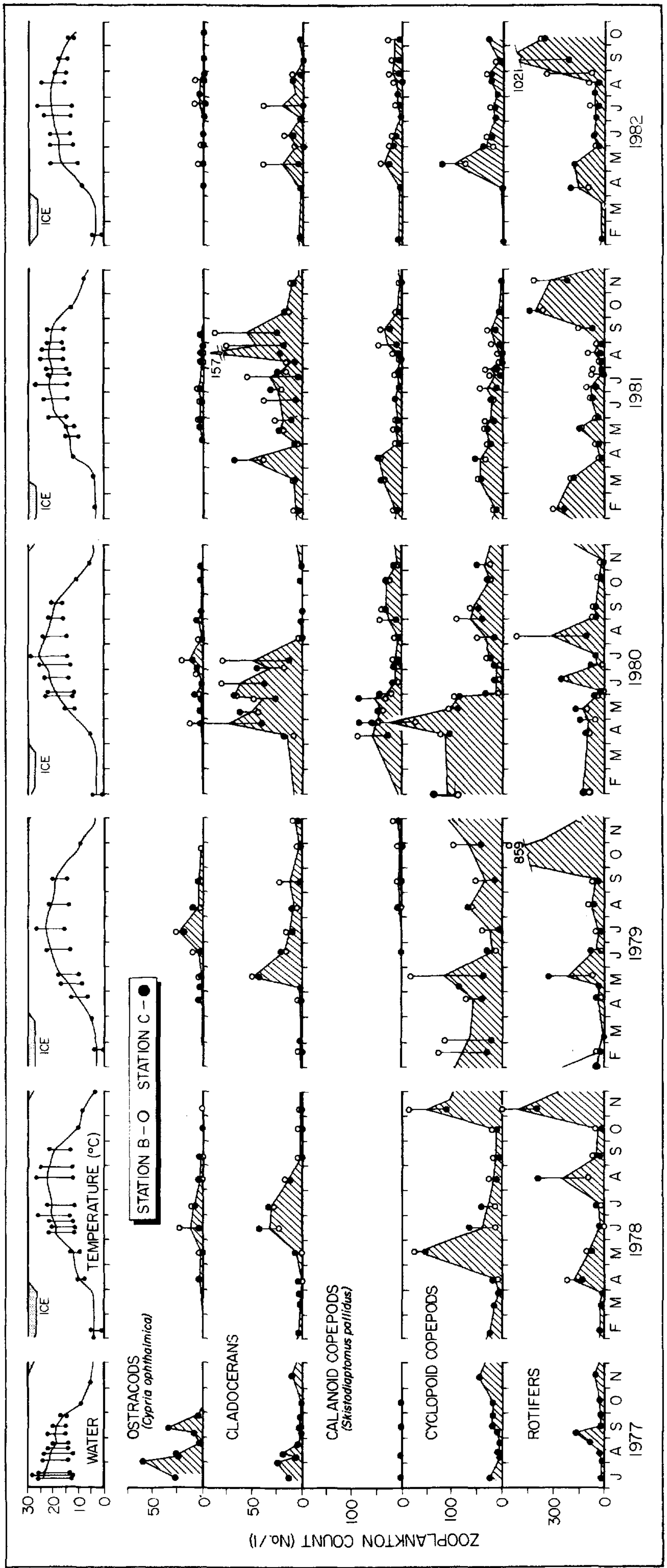

FIGURE 43. *Mean water temperature, ice cover, and mean density of major zooplankton groups netted during 1977-82. Vertical lines connect the temperature extremes or mean densities at Stations B and C on each date.*

Nannoplankton were less abundant, but larger, during warmer months (Table 48). Clumps of blue-green algae could have masked small nannoplankton in the samples, yielding lower counts and higher average biovolumes. Although nannoplankton appeared scarcer and less diverse when blue-green algae exceeded 20,000 cells/ml (Table 49), differences from sparser samples were not significant (unpaired *t*-test). The demise of *Daphnia* was more related to intensive fish predation than to shortages of nannoplankton as food.

Mean chlorophyll-*a* and ^{14}C primary productivity mirrored the seasonal changes in phytoplankton (Figs. 51 and 52). They reached 43 $\pm$ 6 mg/m^3 and 67 $\pm$ 12 mg/m^3 hour, respectively, in August. Highest summer values occurred in 1977 and 1980. The unusually low chlorophyll-*a* values in August 1979 suggest a sampling or measurement error. Sample variances among depths were greatest in summer, when blue-green algae congregated near the water surface. Chlorophyll-*a* and primary productivity were lowest in winter. Differences between Stations B and C were usually not significant (paired *t*-tests).

Water clarity deteriorated as blue-green algal blooms developed, while dissolved color of the water remained below 10 Pt units. Secchi disk visibility declined from 4-5 m in May-June to 0.6 m in July-August. It remained above 1 m through 1982, however, when water stargrass persisted until fall overturn. Secchi disk visibility and mean total phosphorus (P) were each highly correlated with all phytoplankton parameters (Table 50).

Total nitrogen (N)/total P ratios were typically above 20 during summer, suggesting a relative shortage of P. Over 90% of the total N, however, was organic. This fraction is poorly assimilated by algae. Nitrogen fixers (*Anabaena* and *Aphanizomenon*) accounted for one-half of all blue-green algae. Those algae incapable of nitrogen fixation could have been limited by both phosphorus and nitrogen.

Runoff and macrophyte senescence appeared to provide the nutrients needed to drive summer blooms of blue-green algae. Early runoff failed to stimulate blooms until macrophytes decayed. Algal blooms were delayed in 1977 until August, following heavy rains in mid-July (200 mm) and die-off of pondweeds. They were delayed again in 1982 until September, when water stargrass senesced. Ample rain fell in May and June 1978 (300 mm), but failed to stimulate algal blooms until the pondweeds began to decline. Blue-green algae reached 22,000 cells/ml in June 1981, after about 70% of the macrophyte biomass was har-

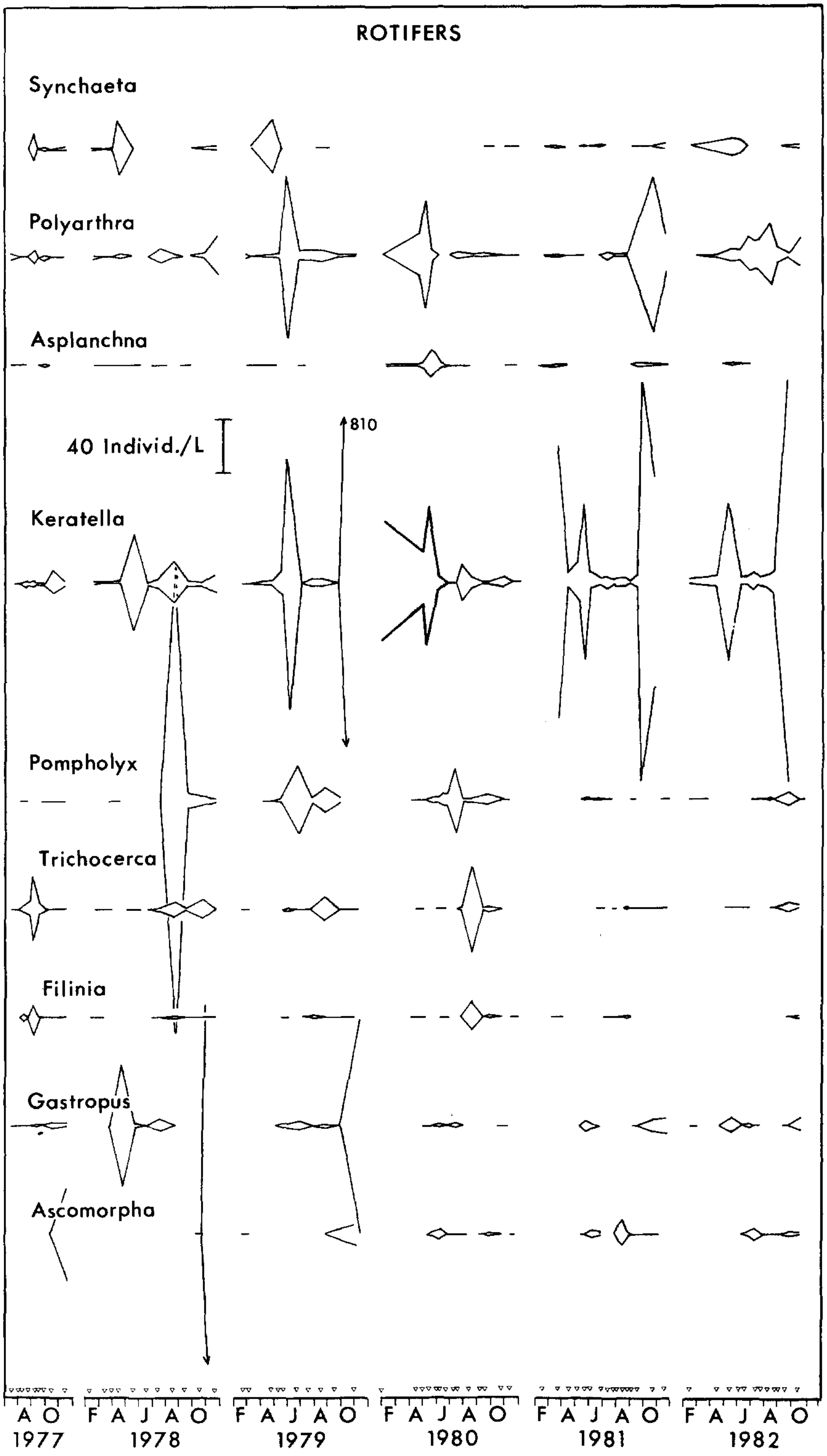

FIGURE 44. *Abundance of rotifers at Station C during 1977-82 (72 sampling dates).*

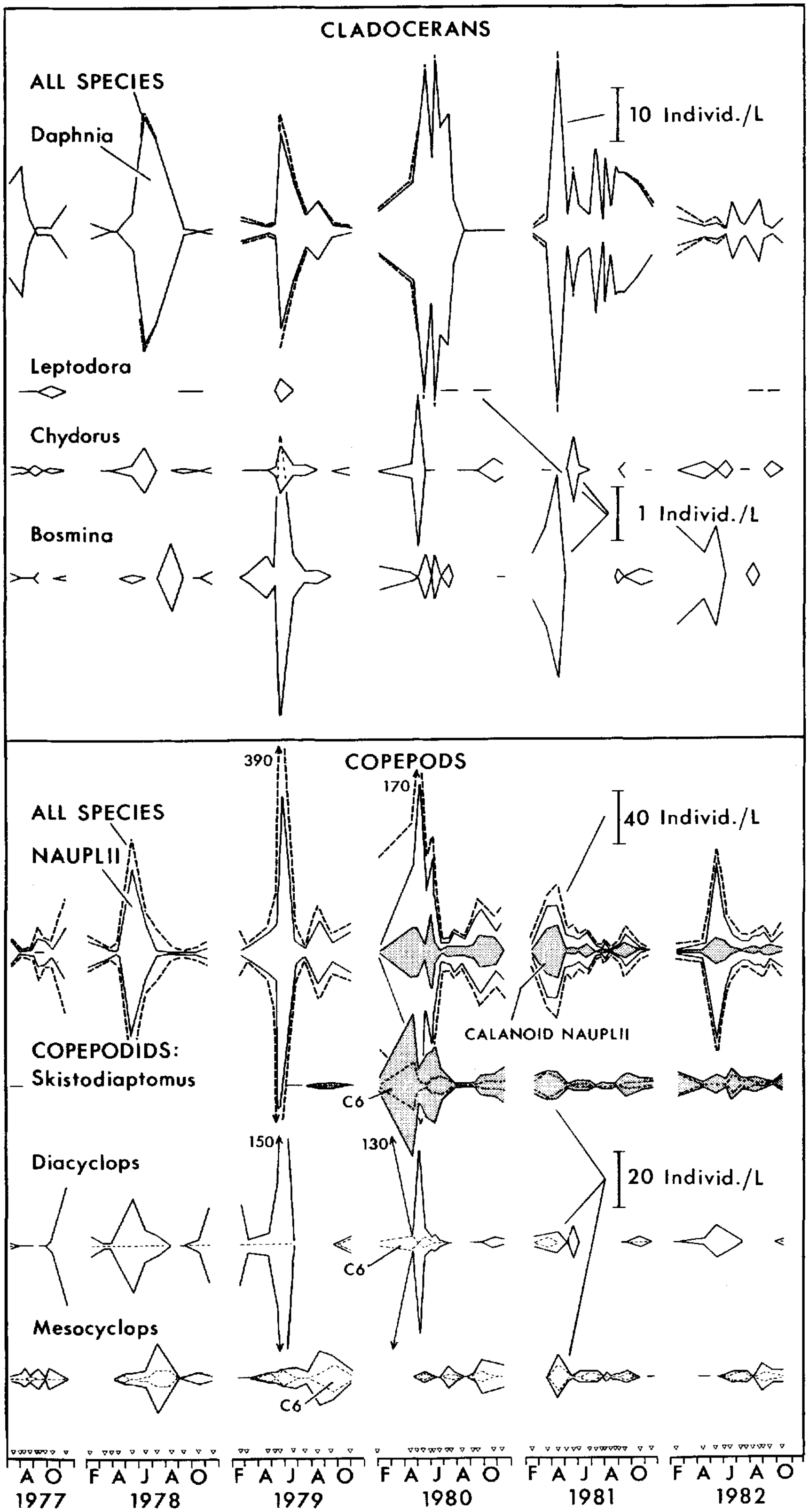

FIGURE 45. *Abundance of cladocerans and copepods during 1977-82. Adult copepods (C6) are designated on lower plots by thin dashed lines; calanoids are differentiated by shading. Note differences in scale size among plots.*

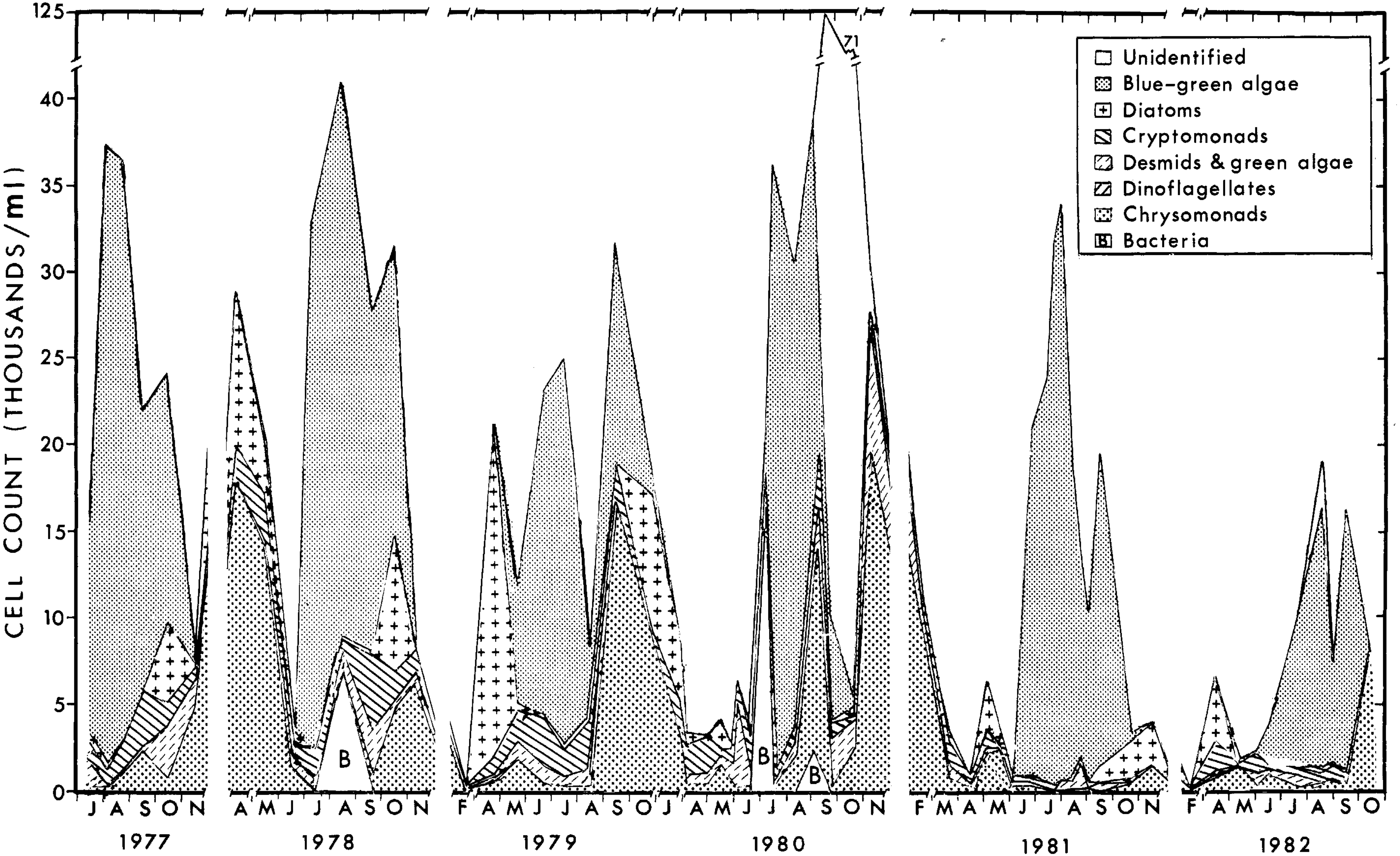

FIGURE 46. *Cell density of major phytoplankton groups during 1977-82.*

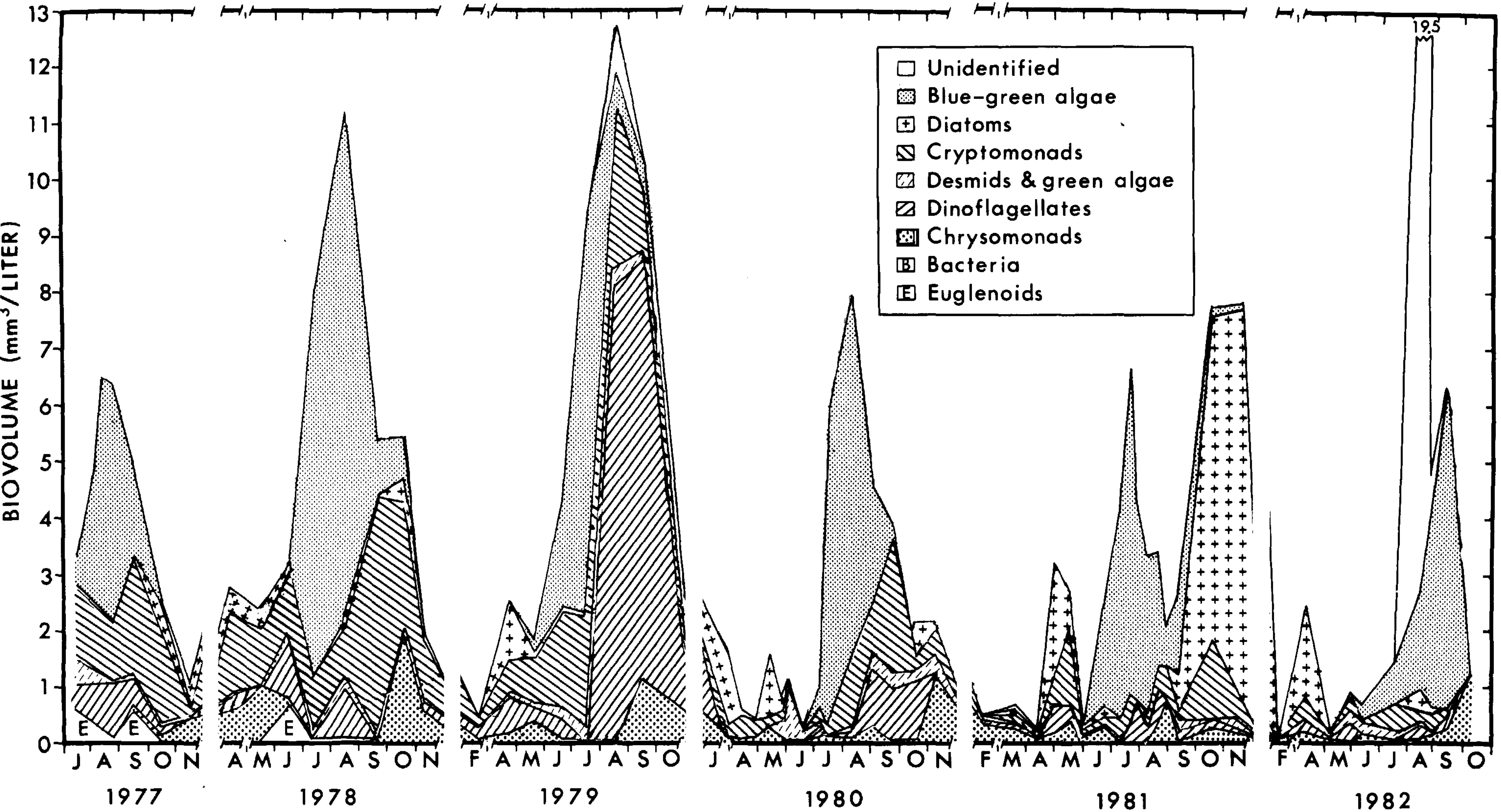

FIGURE 47. *Biovolume of major phytoplankton groups during 1977-82.*

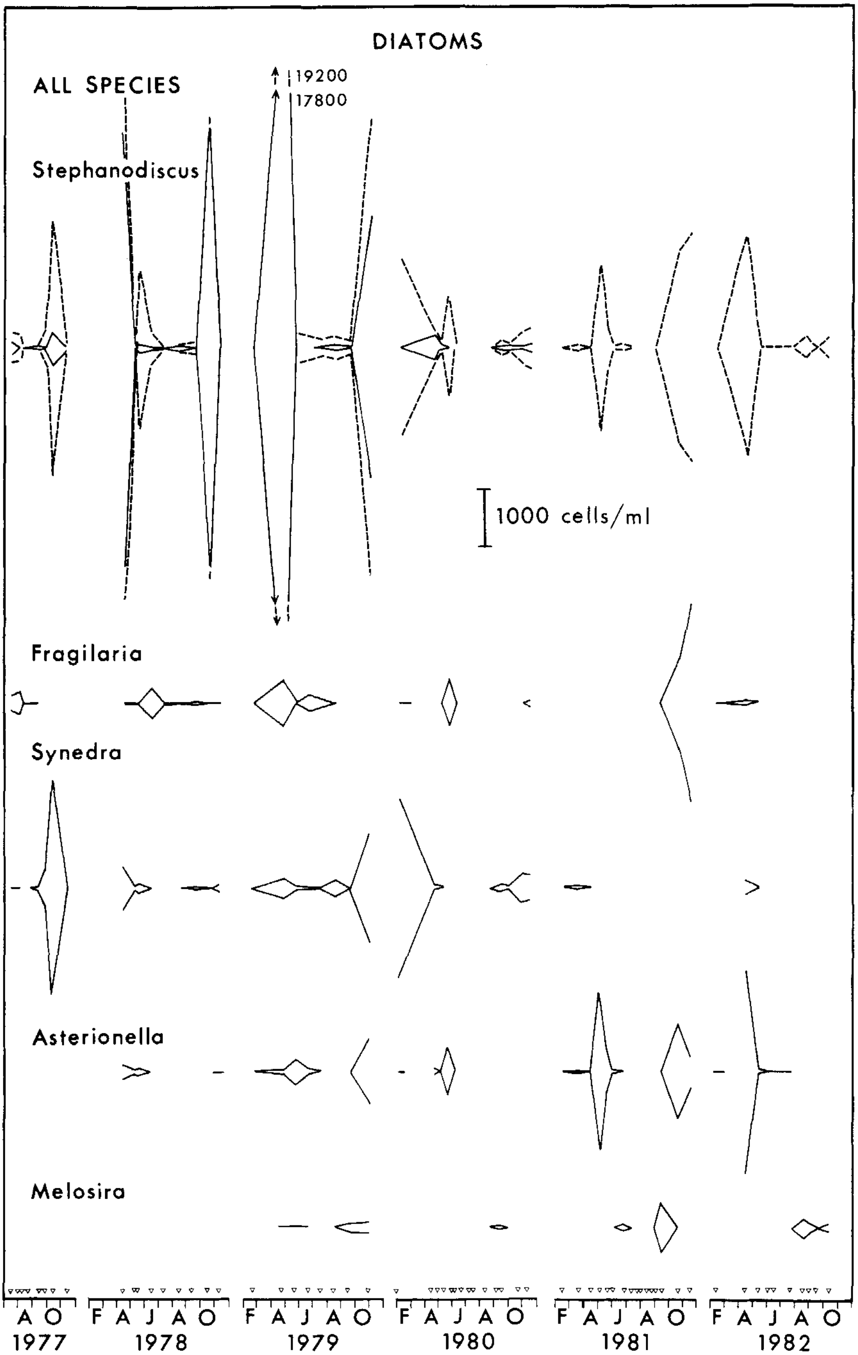

FIGURE 48. *Cell density of diatoms at Station C during 1977-82 (65 sampling dates).*

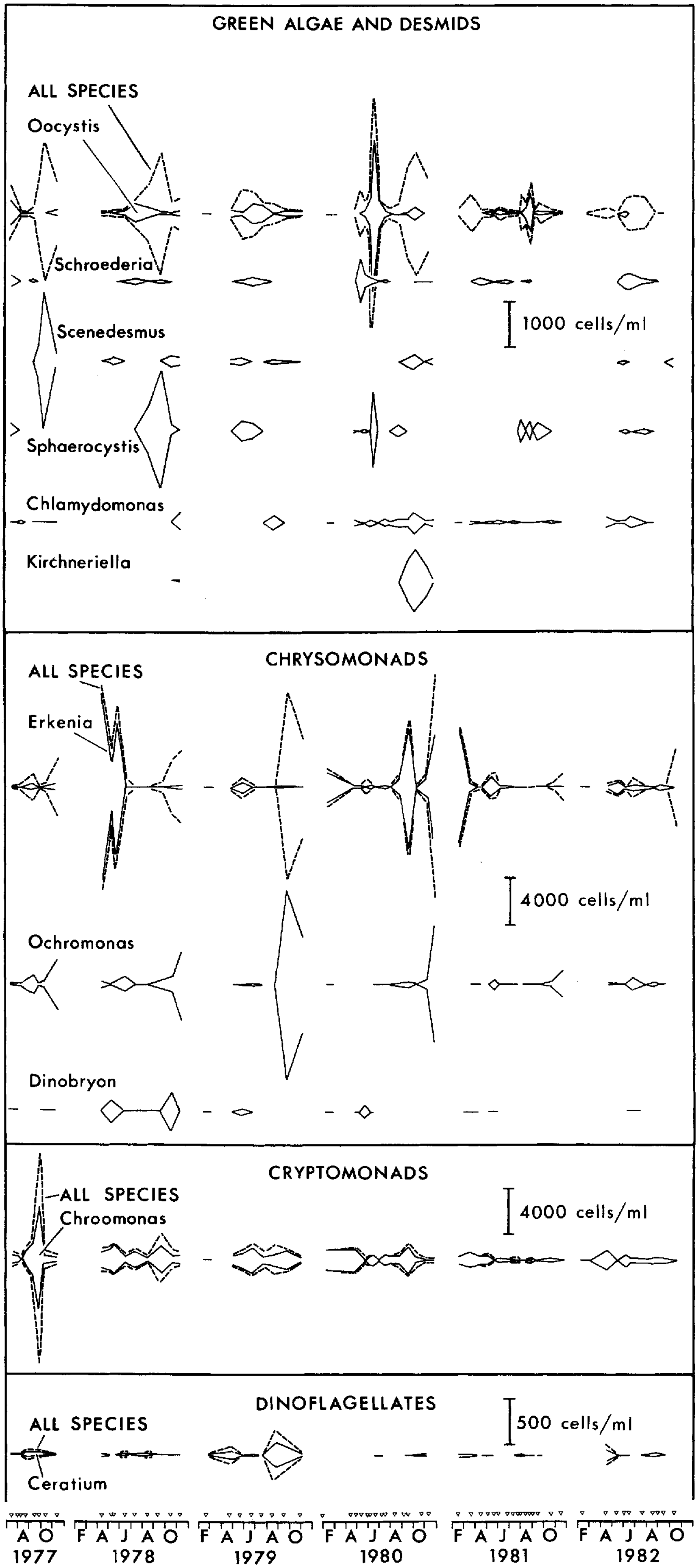

FIGURE 49. *Cell density of green algae and desmids and other flagellates during 1977-82. Note differences in scale size among groups.*

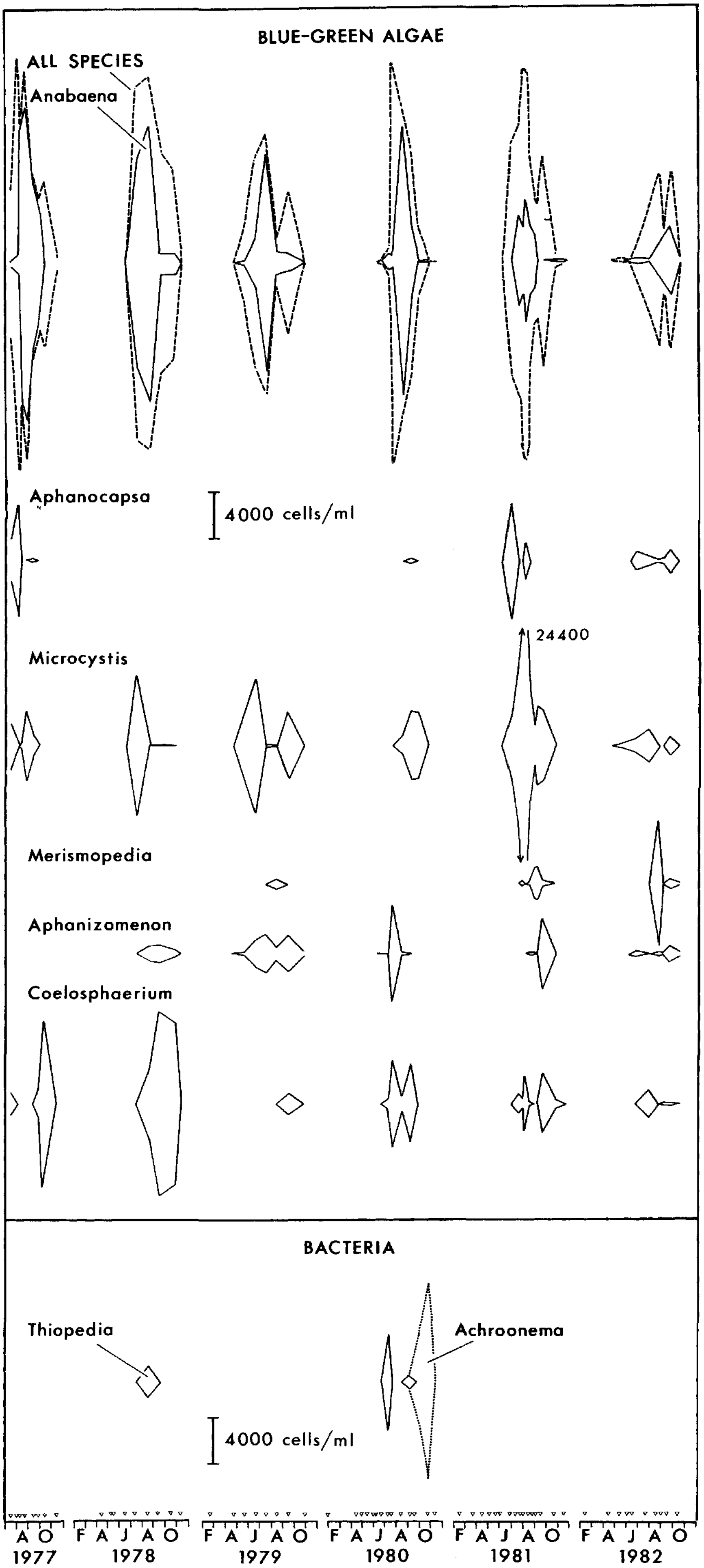

FIGURE 50. *Cell density of blue-green algae and bacteria during 1977-82.*

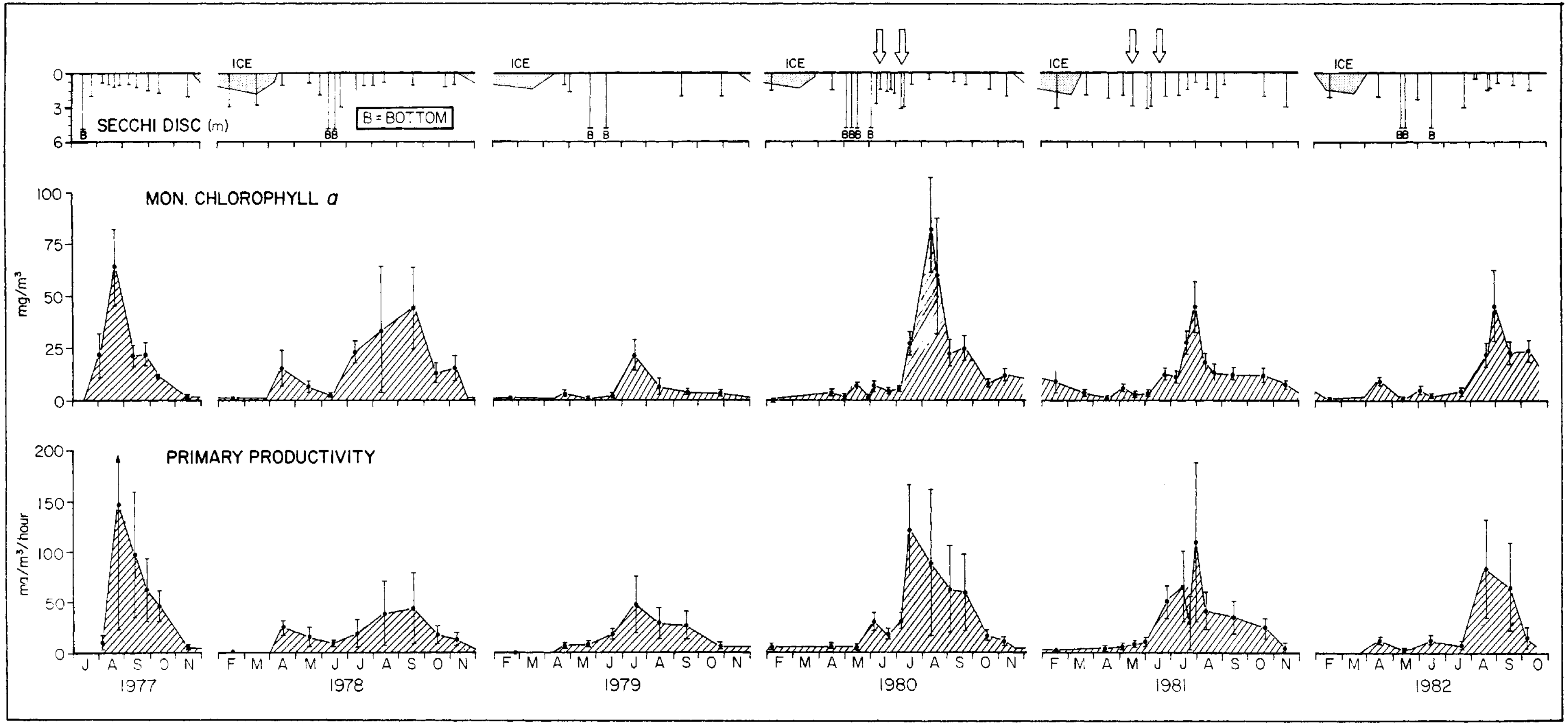

FIGURE 51. *Secchi disk limit of visibility, ice cover, mean monochromatic chlorophyll-*a*, and mean ^{14}C primary productivity at Station B. Secchi disks visible on the bottom at 4.1 m are denoted by B. Vertical bars are ± 1 SE. Means are volume-weighted for 0.5-3.5 m depths.*

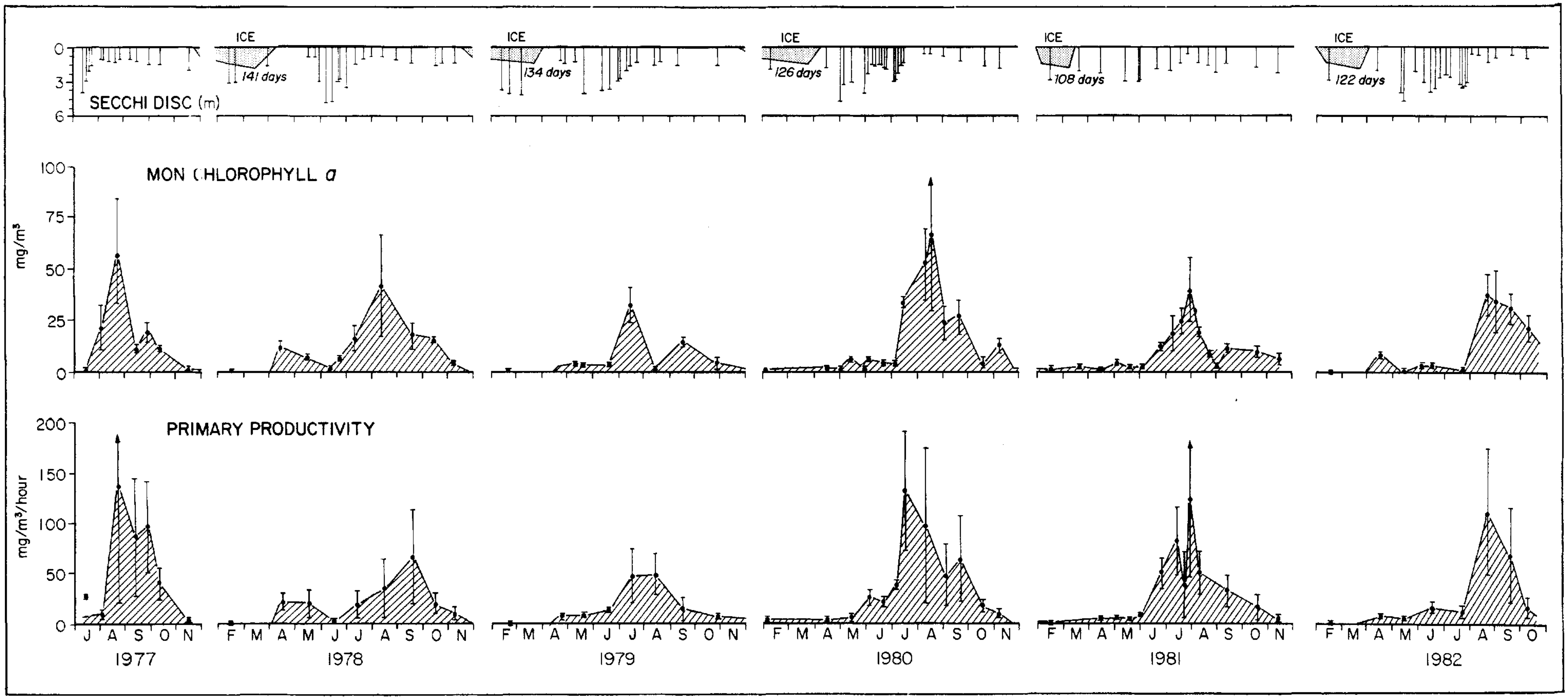

FIGURE 52. *Secchi disk limit of visibility, ice cover, mean monochromatic chlorophyll-a, and mean ^{14}C primary productivity at Station C. No Secchi disks were visible on the bottom at 6.4 m. Other symbols are identical to Station B.*

TABLE 48. *Cell count and biovolume (mean ± 1 SE) of nannoplankton and blue-green algae during 1977-82.*

Taxon	Feb	Apr-May	Jun-Aug	Oct-Nov
Cell count (hundreds/ml)				
Nannoplankton	41 ± 27	69 ± 22	25 ± 6	116 ± 38
Blue-green algae	0	5 ± 5	174 ± 28	38 ± 22
Biovolume (mm^3/L)10				
Nannoplankton	3 ± 1	9 ± 2	17 ± 7	13 ± 3
Blue-green algae	0	tr[a]	29 ± 5	2 ± 1
No. samples	4	14	27	10

[a] tr = less than (0.5 mm^3/L)10.

TABLE 49. *Nannoplankton abundance and species diversity (mean ± 1 SE) in July and August samples differing in concentration of blue-green algae.*

	Blue-green Algae (cells/ml)	
Parameter	Less Than 20,000	More Than 20,000
Cell count (thousands/ml)	4.1 ± 2.0	2.1 ± 0.6
SW diversity ($\log_2$)	2.6 ± 0.2	2.2 ± 0.2
Percent evenness	69 ± 4	67 ± 4
No. samples	8	11

TABLE 50. *Log-log correlation coefficients of phytoplankton vs. total phosphorus (P) or Secchi disk visibility for mid-May to mid-September 1977-82.*[a]

Abiotic	Correlation Coefficient (No. Paired Observations)			
Variable	Chlorophyll	Productivity	Biovolume	Cell Count
Total P	0.75 (54)	0.56 (55)	0.52 (31)	0.45 (31)
Secchi disk	-0.86 (68)	-0.60 (59)	-0.62 (37)	-0.67 (37)

[a] All coefficients are highly significant ($P < 0.01$).

vested, compared to 2,500 cells/ml in June 1980, when 30% was removed. Cumulated rainfall in June of these years was identical (100 mm).

Submerged macrophytes evidentially acted as a nutrient sink in late spring and early summer and, consequently, delayed the onset of blue-green algal blooms. Runoff was effective in stimulating summer blooms only after the macrophytes began to decline. Clear water and reduced summer phytoplankton have been observed in fertile lakes crowded with submerged macrophytes (Pokrovskaya 1983, Canfield et al. 1984). Enough nutrients can be released from senescing macrophytes, however, to stimulate phytoplankton blooms (Carpenter 1980*a*, Landers 1982). The timing of nutrient runoff and the condition of macrophytes can be crucial to algal production in certain lakes.

SUMMARY

MACROPHYTE COMMUNITY STRUCTURE

1. The macrophyte community comprised 9 emergent and 19 submerged or floating species. Cattail, cut-grass, slender spikerush, and softstem bulrush prevailed along shore. They cast shade, trapped sediments, interrupted waves, and created pockets for unattached plants. Coontail, filamentous algae (cladophora and spirogyra), pondweeds (Berchtold's, bushy, curly-leaf, and sago), and water stargrass variously dominated offshore.

2. Growth resumed at ice-out. Cladophora spread along the lake bottom in deep water. Spirogyra rose to the water surface, where its floating mats avoided shade from diatom blooms and pondweeds and formed microhabitats for some macroinvertebrates.

3. Total standing crop attained 130-200 g/m^2 (dry weight) in July, when Berchtold's and sago pondweeds dominated. Water stargrass dominated after 1981. Curly-leaf pondweed declined in July, other pondweeds senesced in August, leaving coontail and water stargrass. Species succession remained incomplete, as openings and channels persisted where plants decayed.

4. Macrophytes propagated from fragments and runners during ice-free periods, but depended on turions, rhizomes, seeds, or tubers in winter.

5. Macrophytes covered 40-70% of the lake bottom, 20-30% of the water surface, by late July. Plant harvesting reduced the surface and midwater growth, leaving the bottom still carpeted.

6. Vegetation was distributed in three overlapping zones. A marginal or shore

zone of emergent plants occurred in water 0-0.3 m deep. A shallow-water zone, covering nearly all of the littoral region and including over 90% of the underwater biomass, extended to 3.5-4.0 m depths. A sparse deep-water zone of cladophora, nitella, and water stargrass stretched from 2.5 to 4.0 m deep.

7. Macrophyte beds were vertically stratified. A canopy, dominated by sago pondweed and some filamentous algae, extended 10-15 m offshore and reached 60 cm thick. It covered a middle layer of much denser vegetation, reaching a depth of 3.5 m and dominated by pondweeds or water stargrass. An inconspicuous layer of bushy pondweed, coontail, elodea, water stargrass, and neophytes of other species grew at the base of taller vegetation. The stratification superficially resembled that in rain forests and served to distribute foliage more efficiently, create microhabitats, and buffer mechanical disturbances.

8. Plant growth was partly restricted along shore by bottom scouring during ice-out, breaking waves during storms, heavy sedimentation from bank erosion or inflowing streams, shading from trees and high banks, and high water temperatures in summer. Macrophytes, in turn, modified the microclimate inshore by restricting water circulation and light penetration. The lake water in summer remained cool beneath the canopy foliage, but warm above it.

9. Nutrient concentrations in whole macrophyte tissues provided little evidence that nutrients limited plant growth.

BOTTOM AND PLANT DWELLING FAUNA

1. An Ekman dredge, plant nets, and multiple-plate samplers together collected 144 species of macroinvertebrates. Insects comprised 75% of species and 50% of individuals. Most species were rare, with 40 species occurring once and only 34 others ever comprising at least 5% of individuals.

2. Many species occupied several habitats. Submerged macrophytes (78 species) and the lake bottom (61) were principal habitats, whereas the open water (33), floating algal mats (7), and the water surface (5) were more restricted.

3. Three-fourths of the bottom fauna occurred inshore during summer. Clams, *Gyraulus* snails, tubificid worms, and chironomid and ceratopogonid larvae predominated. The fauna dispersed during other months. Largest populations occurred in winter when emergence, development, fish predation, and bottom disturbances were minimal.

4. An abundant and diverse fauna developed in and beneath submerged macrophytes. Fewer bottom organisms occurred at Station 5 than elsewhere inshore, until water stargrass invaded in 1982. The submerged macrophytes averaged 31 organisms/g dry weight of plant, with the fauna differing little among macrophyte species. Amphipods, *Physella* snails, naidid worms, beetles, true bugs, water mites, and larvae of chironomids, caddisflies, and mayflies predominated on plants.

5. Over 70% of macroinvertebrate taxa were reported as collectors or shredders of algae and detritus. Macrophytes functioned to annually renew the pool of detritus and to shelter benthos and their prey.

FISH USE OF HABITAT AND FOOD

1. Largemouth bass and bluegills congregated near shore in summer, while black crappies remained offshore. Submerged macrophytes sheltered small fishes (under 120 mm), while restricting larger ones. Cruising lanes opened to all fishes as macrophytes decayed.

2. Fish diets overlapped in spring, but partially segregated in summer. All fish species heavily grazed chironomid larvae and *Daphnia* in spring. Crappies remained zooplanktivores throughout summer, while bass and bluegills grazed larger prey on the lake bottom and macrophytes. Bluegills consumed mayfly and caddisfly larvae, water mites, snails, vegetation, and bryozoans; bass ate mayfly larvae, dragonflies, true bugs, oligochaetes, and fishes. Vascular plants formed 20% by volume of the bluegill diet in July and August.

3. Fishes grew rapidly through their third year (age II), reaching a (mean $\pm$ 95% CL) total length of 223 $\pm$ 5 mm for bass, 212 $\pm$ 22 mm for crappies, and 136 $\pm$ 2 mm for bluegills. Growth of crappies was above average, bluegills average, and bass below average compared to 10 studies of 300 lakes in the Midwest. Bass grew slowly in waters of dense vegetation; bluegill growth was more varied.

4. Fishes grew faster in weight than in length, as indicated by (log-log) length-weight regression slopes in October of 3.2 for bass, 3.4 for bluegills, and 3.7 for crappies. Mean condition factor was highest in June or July for bluegills (1.9-9.2) and bass (1.3-1.5).

5. Bluegills over 49 mm were usually 3-5 times as numerous as bass in October, but fluctuated widely among years. Annual standing crop was 46 $\pm$ 11 kg/ha for bluegills and 16 $\pm$ 3 kg/ha for bass over 49 mm.

INTERACTIONS WITH PLANKTON

1. Diverse zooplankton and phytoplankton communities, partly originating from shore, assembled in the pelagic region. Rotifers comprised 50% of the 72 species of zooplankton netted. Green algae accounted for 40% of the 114 phytoplankton species in Kemmerer samples. Nannoplankton (flagellates, diatoms, and bacteria under 35 μm) contributed one-half of all algae sampled, leaving an equal number too large for most zooplankton to graze. Only 20% of all net zooplankton were large enough (over 0.9 mm) to be consumed by fishes. Much of the secondary production in the pelagic region, consequently, went unutilized by these predators.

2. Spring and fall samples were dominated by copepods (*Diacyclops* and *Skistodiaptomus*), rotifers, and nannoplankton. Other copepods (*Mesocyclops*), cladocerans (*Daphnia*), and blue-green algae (chiefly *Anabaena* and *Microcystis*) amassed in summer. Phytoplankton total counts (24,000 $\pm$ 4,000 cells/ml), total biovolumes (9 $\pm$ 2 mm^3/L), mean chlorophyll-*a* (43 $\pm$ 6 mg/m^3), and mean ^{14}C primary productivity (67 $\pm$ 12 mg/m^3/hour) usually peaked in August. These parameters were highly correlated with Secchi disk visibility and total P. Senescence of submerged macrophytes appeared necessary for production of dense blue-green algal blooms in summer.

CONCLUSIONS

THE DOMINANCE OF MACROPHYTES

A dynamic community of macrophytes, coupling structure with function, developed in Halverson Lake. The finely branched foliage maximized biomass and habitat structure. Horizontal zonation distributed the biomass toward deep water. The expansive foliage intercepted runoff, stored nutrients, buffered water movements, and stabilized sediments. Species succession channelized and diversified the community. Floating mats of algae formed microhabitats for benthos in spring. Plant beds gradually became more accessible to fishes. Sago pondweed shaded understory plants. The foliage vertically stratified into a three-dimensional labyrinth. Rather than a confusing entanglement, the macrophyte community appeared intricately structured.

The littoral region teemed with species. Macrophytes were habitat for colonizing invertebrates and algae. Many macroinvertebrate species recurred in low numbers. Rareness can be adaptive in filling niches and reducing encounters with predators. Abundant taxa occupied both macrophytes and the lake bottom. Diet and habitat preferences broadly overlapped. Most taxa consumed detritus and algae, occupying more than one trophic level. Some carnivorous insects even ingested detritus with carrion and live prey. Dead macrophytes refueled the pool of detritus. Reliance on detritus as food lengthened food chains, by requiring a decomposer step. Energy and materials could then be recycled to the predator-prey food web.

Submerged macrophytes sheltered small bass and bluegills, but restricted large bass (over 179 mm) offshore with crappies. Diets broadly overlapped, as fishes utilized common prey on both the macrophytes and bottom inshore. Even large bass grazed macroinvertebrates. Food became partially segregated by predator size as plant beds developed. Macrophytes expanded feeding opportunities by supporting a wide range of prey. This diversified the energy pathways leading to secondary production. Emergence of chironomid larvae and depletion of *Daphnia* in early summer, however, forced bluegills to progressively switch prey and consume more vegetation. Access to forage fishes inshore appeared crucial to continued growth of bass.

The plankton was enriched with species from shore, especially rotifers and green algae. Many phytoplankton appeared too large for invertebrate predators, whereas most net zooplankton were too small for fishes. This left secondary production directly underutilized by predators in the pelagic region. By storing nutrients during spring and early summer, submerged macrophytes delayed blue-green algal blooms. Nutrients became available to drive summer blooms mainly when submerged macrophytes senesced.

The macrophyte community ultimately dominated life in Halverson Lake. The diversity, community structure, and seasonal changes of macrophytes were linked to interactions with benthos, fishes, and plankton. Creating microhabitats, renewing detritus, screening fishes, storing nutrients, and buffering water movements were important functions of macrophytes. The study illustrates how the macrophyte community can play a pivotal role in the ecology of a shallow water lake.

MANAGING WITH MACROPHYTES

When submerged macrophytes dominate a lake their value as a resource can conflict with demands for boating and swimming. Macrophyte interactions in Halverson Lake suggest how defoliating lake shallows can disrupt plant community structure, expose sediments to different plant species, eliminate macroinvertebrate habitat, and deprive fishes of prey and cover. Avoiding such multifarious impacts requires thoughtful planning, an integrated approach, and a concept of the littoral region as a vibrant interactive unit.

Littoral regions can be restructured to enhance recreation, without sacrificing biological diversity. Fragmenting a wall of dense vegetation permits anglers and game fishes freer access to inshore habitat. Such macrophyte beds of moderate density maximize fish growth (Crowder and Cooper 1982). Selective plant harvesting in Halverson Lake created fish cruising lanes, but removable fiberglass screens can channelize foliage too shallow or deep for a harvester (Engel 1984). Cedar trees by Halverson Lake reduced shoreline growth, suggesting that intentional plantings along south and west banks of lakes can provide an attractive long-term control of shallow plants. Spot dredging and selective riprapping can fashion plant-free strips along shore.

Attractive and useful underwater gardens are possible in lakes with little vegetation. Water lily beds, grown from tuberous rootstocks, provide cover for adult bass. Dense monotypic stands of fine-leaved plants can be diversified with cuttings of broad-leaved pondweeds or tubers of wild celery. Shoots of narrow-leaved pondweeds and coontail, harboring a plethora of aquatic insects in Halverson Lake, are edible to waterfowl. Grown near appropriate emergent cover on shore, such plantings can improve habitat for a variety of wildlife and fishes.

Restructuring littoral regions is an architectural approach that builds from a phased lake-use plan. The lake is zoned into areas of similar function. A management strategy is then tailored to each zone. Zones need not be contiguous. Priority ones are managed first. Some zones are kept plant-free for swimming or boating, including boat lanes radiating from shore. Areas of open variegated macrophyte beds are constructed for angling. Zones of dense vegetation can become fish or waterfowl nurseries. Some zones are left unmanaged, until they are needed or funds become available. Different management techniques can, therefore, be phased in over time.

Managing with macrophytes, rather than repeatedly destroying them, can provide a balanced approach to lake rehabilitation. A plan to manage selected areas of a lake can even economize on total treatment costs.

GLOSSARY

ASSOCIATION — a unit of vegetation comprising several co-dominant species.

BENTHOS — organisms living in or on the bottom, macrophytes, or other solid substrates of a lake or stream.

BIOMASS OF MACROPHYTES — weight of cleaned foliage, including runners but not roots, dried in an oven at 105 C.

BIOVOLUME OF ALGAE — total volume of an alga, including all its cells (if multicellular) and extracellular material.

COPEPODID — a juvenile or adult copepod developing after the naupliar (larval) stages.

DETRITUS — organic and inorganic remains of plants and animals suspended in water or settled on the bottom and adjoining objects of a lake or stream.

EPIPELIC ALGAE — algae growing on sediments or objects on a lake or stream bottom.

EPIPLEUSTON — organisms living at the surface tension layer of water.

EULITTORAL ZONE — a region along shore where waves break.

FLUOR — a chemical solution used to measure the radioactivity of a sample.

GASTRIC LAVAGE — a method to flush food from fishes with jets of water.

INSTAR — a stage between molts of developing crustaceans and insects.

LITTORI-PROFUNDAL ZONE — a region of a lake where vascular plants give way to filamentous macroscopic algae.

MACROPHYTES — macroscopic plants, including vascular plants (angiosperms), stoneworts (chara and nitella), and filamentous macroscopic algae.

MEROPLANKTON — benthic organisms temporarily occupying the plankton.

NANNOPLANKTON — plankton small enough to pass through a net.

QUENCHING — loss of radioactivity in samples to be measured.

S/cm — Siemens/cm, a unit of electrical conductivity equivalent to micromhos/cm.

TURION — a resistant dormant bud on shoots of certain aquatic vascular plants.

LITERATURE CITED

ABRAMS, P.
1980. Some comments on measuring niche overlap. Ecology 61:44-49.
1982. Reply to a comment by Hurlbert. Ecology 63:252-54.

ADAMS, M. S. AND R. T. PRENTKI
1982. Biology, metabolism and functions of littoral submersed weedbeds in Lake Wingra, Wisconsin, USA: a summary and review. Arch. Hydrobiol. Suppl. 62:333-409.

AIKEN, S. G. AND K. F. WALZ
1979. Turions of *Myriophyllum exalbescens*. Aquat. Bot. 6:357-63.

ALLEE, W. C.
1912. Seasonal succession in old forest ponds. Trans. Ill. Acad. Sci. 4. 4 pp.

AMERICAN PUBLIC HEALTH ASSOCIATION
1976. Standard methods for the examination of water and wastewater, 14th ed. Am. Public Health Assoc., Washington, D.C. 1193 pp.

ANDREWS, J. D. AND A. D. HASLER
1943. Fluctuations in the animal populations of the littoral zone in Lake Mendota. Wis. Acad. Sci., Arts, and Lett. 35:175-85.

ANTON, A. AND H. C. DUTHIE
1981. Use of cluster analysis in the systematics of the algal genus *Cryptomonas*. Can. J. Bot. 59:992-1002.

APPLEGATE, R. L., J. W. MULLAN, AND D. I. MORAIS
1966. Food and growth of six centrarchids from shoreline areas of Bull Shoals Reservoir. Proc. Southeast Assoc. Game and Fish Comm. 20:469-82.

BAKER, F. C.
1928. The fresh water Mollusca of Wisconsin, Part I. Gastropoda. Trans. Wis. Acad. Sci., Arts, and Lett. 70:1-507.

BALL, R. C.
1948. Relationship between available fish food, feeding habits of fish and total fish production in a Michigan lake. Mich. State Coll. Agric. Exp. Stn. Bull. 206. 59 pp.

BARNES, R. D.
1974. Invertebrate zoology, 3rd ed. W. B. Saunders, Philadelphia, Pa. 870 pp.

BAUMANN, P. C. AND J. F. KITCHELL
1974. Diel patterns of distribution and feeding of bluegill (*Lepomis macrochirus*) in Lake Wingra, Wisconsin. Trans. Am. Fish. Soc. 103:255-60.

BEARD, T. D.
1973. Overwinter drawdown: impact on the aquatic vegetation in Murphy Flowage, Wisconsin. Wis. Dep. Nat. Resour. Tech. Bull. No. 61. 14 pp.
1982. Population dynamics of young-of-the-year bluegill. Wis. Dep. Nat. Resour. Tech. Bull. No. 127. 32 pp.

BEATTY, L. D. AND F. F. HOOPER
1958. Benthic associations of Sugar-loaf Lake. Mich. Acad. Sci., Arts, and Lett. 43:89-106.

BECKMAN, W. C.
1946. The rate of growth and sex ratio for seven Michigan fishes. Trans. Am. Fish. Soc. 76:63-81.

BELONGER, B. J.
1969. Aquatic plant survey of major lakes in the Fox River (Illinois) watershed. Wis. Dep. Nat. Resour. Res. Rep. No. 39. 60 pp.

BENNETT, G. W.
1937. The growth of the large mouthed black bass, *Huro salmoides* (Lacépède), in the waters of Wisconsin. Copeia 1937:104-18.
1948. The bass-bluegill combination in a small artificial lake. Ill. Nat. Hist. Surv. Bull. 24:376-412.

BENNETT, G. W., D. H. THOMPSON, AND S. A. PARR
1940. Lake management reports. 4. A second year of fisheries investigations at Fork Lake, 1939. Ill. Nat. Hist. Surv. Biol. Notes 14:1-24.

BOYLEN, C. W. AND R. B. SHELDON
1976. Submergent macrophytes: growth under winter ice cover. Science 194:841-42.

BRANDLOVA, J., Z. BRANDL, AND C. H. FERNANDO
1972. The Cladocera of Ontario with remarks on some species and distribution. Can. J. Zool. 50:1373-1403.

BRIGHAM, A. R., W. U. BRIGHAM, AND A. GNILKA, EDS.
1982. Aquatic insects and oligochaetes of North and South Carolina. Midwest Aquat. Enterprises, Mohomet, Ill. 837 pp.

BRINKHURST, R. O. AND B. G. M. JAMIESON
1971. Aquatic Oligochaeta of the world. Univ. Toronto Press. Toronto, Ont. 860 pp.

BRITTON, N. L. AND A. BROWN
1970. An illustrated flora of the northern United States and Canada. Vol. 1. Dover, New York. 680 pp.

BROOKS, J. L.
1957. The systematics of North American *Daphnia*. Mem. Conn. Acad. Arts and Sci. New Haven, Conn. 180 pp.

BUMBY, M. J.
1977. Changes in submerged macrophytes in Green Lake, Wisconsin, from 1921 to 1971. Trans. Wis. Acad. Sci., Arts, and Lett. 65:120-51.

BURCH, J. B.
1972. Freshwater sphaeriacean clams (Mollusca: Pelecypoda) of North America. Biota of Freshwater Ecosystems. Identification Man. 3. U.S. Environ. Prot. Agency, Washington, D.C. 31 pp.
1982. Freshwater snails (Mollusca: Gastropoda) of North America. U.S. Environ. Prot. Agency, Cincinnati, Ohio. 294 pp.

CANFIELD, D. E., JR., J. V. SHIREMAN, D. E. COLLE, W. T. HALLER, C. E. WATKINS, II, AND M. J. MACEINA
1984. Prediction of chlorophyll *a* concentrations in Florida lakes: importance of aquatic macrophytes. Can. J. Fish. Aquat. Sci. 41:497-501.

CARLANDER, K. D.
1977. Handbook of freshwater fishery biology. Iowa State Univ. Press, Ames, Iowa. Vol. 2. 431 pp.

CARPENTER, S. R.
1980*a*. Enrichment of Lake Wingra, Wisconsin, by submersed macrophyte decay. Ecology 61:1145-55.
1980*b*. The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. Can. J. Bot. 58:527-35.

CARR, J. L.
1969. The primary productivity and physiology of *Ceratophyllum demersum*. II. Micro primary productivity, pH, and the P/R ratio (Part I). Austr. J. Mar. Freshw. Res. 20:115-26.

CATTANEO, A. AND J. KALFF
1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. Limnol. Oceanogr. 25:280-89.

CHURCHILL, W. S.
1976. Population and biomass estimates of fishes in Lake Wingra. Wis. Dep. Nat. Resour. Tech. Bull. No. 93. 8 pp.

COOK, E. F.
1956. The Nearctic Chaoborinae (Diptera: Culicidae). Univ. Minn. Agric. Exp. Stn. Tech. Bull. 218. 102 pp.

COOPER, S. D.
1983. Selective predation on cladocerans by common pond insects. Can. J. Zool. 61:879-86.

COUEY, F. M.
1935. Fish food studies of a number of northeastern Wisconsin lakes. Trans. Wis. Acad. Sci., Arts, and Lett. 29:131-72.

COWEY, C. B. AND J. R. SARGENT
1979. Nutrition. pp. 1-69 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, eds. Fish physiology. Vol. 3. Acad. Press. New York. 786 pp.

CROCKER, D. W. AND D. W. BARR
1968. Handbook of the crayfishes of Ontario. Univ. Toronto Press. Toronto, Ont. 158 pp.

CROWDER, L. B. AND W. E. COOPER
1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802-13.

CUMMINS, K. W.
1973. Trophic relations of aquatic insects. Ann. Rev. Entomol. 18:183-206.

1974. Structure and function of stream ecosystems. BioScience 24:631-40.

CURTIS, J. T.
1959. The vegetation of Wisconsin: an ordination of plant communities. Univ. Wis. Press, Madison, Wis. 657 pp.

CZAIKA, S. C.
1982. Identification of nauplii N1-N6 and copepodids CI-CVI of the Great Lakes calanoid and cyclopoid copepods (Calanoida, Cyclopoida, Copepoda). J. Great Lakes Res. 8:439-69.

DALE, H. M. AND T. J. GILLESPIE
1977. The influence of submersed aquatic plants on temperature gradients in shallow water bodies. Can. J. Bot. 55:2216-25.

DALE, H. M. AND G. E. MILLER
1978. Changes in the aquatic macrophyte flora of Whitewater Lake near Sudbury, Ontario from 1947 to 1977. Can. Field-Nat. 92:264-70.

DAWSON, F. H.
1978. Aquatic plant management in semi-natural streams: the role of marginal vegetation. J. Environ. Manage. 6:213-21.

DAWSON, F. H. AND U. KERN-HANSEN
1978. Aquatic weed management in natural streams: the effect of shade by the marginal vegetation. Verh. Int. Verein. Limnol. 20:1451-56.

DEEVEY, E. S., JR. AND G. B. DEEVEY
1971. The American species of *Eubosmina* Seligo (Crustacea, Cladocera). Limnol. Oceanogr. 16:201-18.

DICOSTANZO, C. J.
1957. Growth of bluegill, *Lepomis macrochirus*, and pumpkinseed, *L. gibbosus*, of Clear Lake, Iowa. Iowa State Coll. J. Sci. 32:19-34.

DODSON, S. I.
1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15:131-37.

DOXTATER, G. D.
1964. Food habits of the bluegill as influenced by season and size class. Unpubl. rep. Ind. Dep. Conserv. Div. Fish and Game, Indianapolis, Ind. 14 pp.

DRENNER, R. W., J. R. STRICKLER, AND W. J. O'BRIEN
1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish. Res. Board Can. 35:1370-73.

EDDY, S. AND K. D. CARLANDER
1942. Growth rate studies of Minnesota fishes. Minn. Dep. Conserv. Div. Game and Fish Bur. Fish Res. Invest. Rep. 28. 64 pp.

EDDY, S. AND A. C. HODSON
1961. Taxonomic keys to the common animals of the north central states exclusive of the parasitic worms, insects and birds. Burgess Publ. Co., Minneapolis, Minn. 162 pp.

EDMONDSON, W. T., ED.
1959. Fresh-water biology, 2nd ed. John Wiley and Sons, New York. 1248 pp.

1971. Methods for processing samples and developing data. pp. 127-66 *in* W. T. Edmondson and G. G. Winberg, eds. A manual on methods for the assessment of secondary productivity in fresh waters. Int. Biol. Program. Blackwell Sci. Publ., Oxford, England. Handbook 17. 358 pp.

EDMUNDS, G. F., JR., S. L. JENSEN, AND L. BERNER
1976. The mayflies of North and Central America. Univ. Minn. Press, Minneapolis, Minn. 330 pp.

ENGEL, S.
1979. Ecological interactions between submersed macrophytes and other communities in a small lake. Wis. Dep. Nat. Resour. Perf. Rep. 19 pp. (unpubl. rep.)

1980. Ecological interactions between submersed macrophytes and other communities in a small lake. II. Outcome of the 1980 harvesting. Wis. Dep. Nat. Resour. Perf. Rep. 24 pp. (unpubl. rep.)

1983. Ecological interactions between submersed macrophytes and other communities in a small lake. III. Outcome of the 1981 harvesting. Wis. Dep. Nat. Resour. Prog. Rep. 19 pp. (unpubl. rep.)

1984. Restructuring littoral zones: a different approach to an old problem. pp. 463-66 *in* North Am. Lake Manage. Soc., ed. Lake and reservoir management. U.S. Environ. Prot. Agency Rep. 440/5-84-001. 604 pp.

ENGEL, S. AND S. A. NICHOLS
1984. Lake sediment alteration for macrophyte control. J. Aquat. Plant Manage. 22:38-41.

ETNIER, D. A.
1971. Food of three species of sunfishes (*Lepomis*, Centrarchidae) and their hybrids in three Minnesota lakes. Trans. Am. Fish. Soc. 10:124-28.

FASSETT, N. C.
1930. The plants of some northeastern Wisconsin lakes. Trans. Wis. Acad. Sci., Arts, and Lett. 25:157-68.

1966. A manual of aquatic plants. Univ. Wis. Press, Madison, Wis. 405 pp.

FEDOROV, A. A.
1966. The structure of the tropical rain forest and speciation in the humid tropics. J. Ecol. 54:1-11.

FERRIS, V. R., L. M. FERRIS, AND J. P. TJEPKEMA
1976. Genera of freshwater nematodes (Nematoda) of eastern North America. U.S. Environ. Prot. Agency, Cincinnati, Ohio. 38 pp.

FLEMER, D. A. AND W. S. WOOLCOTT
1966. Food habits and distribution of the fishes of Tuckahoe Creek, Virginia, with special emphasis on the bluegill, *Lepomis m. macrochirus* Rafinesque. Chesapeake Sci. 7:75-89.

FORBES, S. A. AND R. E. RICHARDSON
1920. The fishes of Illinois, 2nd ed. Ill. Nat. Hist. Surv., Springfield, Ohio. 357 pp.

FOREST, H. S.
1977. Study of submerged aquatic vascular plants in northern glacial lakes (New York state, U.S.A.). Folia Geobot. Phytotax., Praha 12:329-41.

FOSTER, J. R.
1977. Pulsed gastric lavage: an efficient method of removing the stomach contents of live fish. Prog. Fish Cult. 39:166-69.

GEORGE, E. L. AND W. F. HADLEY
1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Trans. Am. Fish. Soc. 108:253-61.

GERKING, S. D.
1962. Production and food utilization in a population of bluegill sunfish. Ecol. Monogr. 32:31-78.

GERLOFF, G. C.
1973. Plant analysis for nutrient assay of natural waters. U.S. Environ. Prot. Agency Rep. R1-73-001. 66 pp.

GERRISH, N. AND J. M. BRISTOW
1979. Macroinvertebrate associations with aquatic macrophytes and artificial substrates. J. Great Lakes Res. 5:69-72.

GILBERT, J. J., C. W. BIRKY, JR. AND E. S. WURDAK
1979. Taxonomic relationships of *Asplanchna brightwelli*, *A. intermedia*, and *A. sieboldi*. Arch. Hydrobiol. 87:224-42.

GLASS, N. R.
1971. Computer analysis of predation energetics in the largemouth bass. pp. 325-63 *in* B. C. Patten, ed. Systems analysis and simulation in ecology. Vol. 1. Acad. Press, New York.

GOODEY, T.
1963. Soil and freshwater nematodes, 2nd ed. rev. by J. B. Goodey. Methuen, London. 544 pp.

GOULDER, R.
1969. Interactions between the rates of production of a freshwater macrophyte and phytoplankton in a pond. Oikos 20:300-09.

HAAG, R. W.
1983. Emergence of seedlings of aquatic macrophytes from lake sediments. Can. J. Bot. 61:148-56.

HANN, B. J.
1980. Population differentiation in the *Eurycercus* (*Bullatifrons*) species complex (Chydoridae, Cladocera) in eastern North America. Indiana Univ. Bloomington. PhD Thesis. 165 pp.

HASLE, G. R.
1978. The inverted-microscope method. pp. 88-96. Using the inverted microscope. pp. 191-96 *in* A. Sournia, ed. Phytoplankton manual. U.N. Educ. Sci. and Cult. Organ. (UNESCO), Paris. 337 pp.

HERBERG, R. J.
1965. Channels ratio method of quench correction in liquid scintillation counting. Packard Instrum. Co., Tech. Bull. 15. 7 pp.

HESTER, F. E. AND J. S. DENDY
1962. A multiple-plate sampler for aquatic macroinvertebrates. Trans. Am. Fish. Soc. 91:420-21.

HILSENHOFF, W. L.
1975. Aquatic insects of Wisconsin, with generic keys and notes on biology, ecology, and distribution. Wis. Dep. Nat. Resour. Tech. Bull. No. 89. 52 pp.

(1981). Aquatic insects of Wisconsin. Keys to Wisconsin genera and notes on biology, distribution and species. Nat. Hist. Counc. Univ. Wis. Madison, Wis. 60 pp.

HILSENHOFF, W. L. AND R. P. NARF
1968. Ecology of Chironomidae, Chaoboridae, and other benthos in fourteen Wisconsin lakes. Ann. Entomol. Soc. Am. 61:1173-81.

HOWELL, H. H., H. S. SWINGLE, AND E. V. SMITH
1941. Bass and bream food in Alabama waters. Ala. Conserv. 11(4):3,12.

HOWMILLER, R.
1975. Identification of Wisconsin Tubificidae. Wis. Dep. Nat. Resour. Res. Rep. No. 80. 5 pp.

HUISH, M. T.
1957. Food habits of three Centrarchidae in Lake George, Florida. Proc. Southeast Assoc. Game and Fish Comm. 11:293-302.

HUNGERFORD, H. B.
1948. The Corixidae of the western hemisphere (Hemiptera). Univ. Kans. Sci. Bull. 32:1-827. (1977 printing).

HUTCHINSON, G. E.
1975. A treatise on limnology. Limnological botany. Vol. 3. Wiley-Interscience, John Wiley and Sons, New York. 660 pp.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Conn. 302 pp. (trans. from Russian).

JORGA, W., W.-D. HEYM, AND G. WEISE
1982. Shading as a measure to prevent mass development of submersed macrophytes. Int. Revue Ges. Hydrobiol. 67:271-81.

KEAST, A.
1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. Environ. Biol. Fish. 3:7-31.

KEAST, A., J. HARKER, AND D. TURNBULL
1978. Nearshore fish habitat utilization and species associations in Lake Opinicon (Ontario, Canada). Environ. Biol. Fish. 3:173-84.

KITCHELL, J. F. AND J. T. WINDELL
1970. Nutritional value of algae to bluegill sunfish, *Lepomis macrochirus*. Copeia 1970:186-90.

KLEMM, D. J.
1972. Freshwater ecosystems (Annelida: Hirudinea) of North America. Biota of freshwater ecosystems. Identification Man. 2. U.S. Environ. Prot. Agency, Washington, D.C. 53 pp.

KLINGELHOETS, A. J.
1962. Soil survey of Iowa County, Wisconsin. U.S. Dep. Soil Conserv. Serv. Ser. 1958(22). 101 pp.

KMIOTEK, S. AND C. L. CLINE
1952. Growth of southern Wisconsin largemouth bass with creel census results from lakes with liberalized regulations. Wis. Conserv. Dep. Fish. Invest. Rep. 670. 11 pp.

KOFOID, C. A.
1903. The plankton of the Illinois River, 1894-1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part I. Quantitative investigations and general results. Ill. Lab. Nat. Hist. Bull. 6:95-629.

KOGAN, S. I.
1972. Some biological peculiarities in reservoirs of South Turkmenia. Verh. Int. Verein. Limnol. 18:867-71.

KOLLMAN, A. L. AND M. K. WALI
1976. Intraseasonal variations in environmental and productivity relations of *Potamogeton pectinatus* communities. Arch. Hydrobiol. Suppl. 50(4):439-72.

KOŘÍNEK, V.
1971. Comparative study of the head pores in the genus *Bosmina* Baird (Crustacea, Cladocera). Věstník Československ. Společ. Zool. 4:275-96.

KOŘÍNKOVÁ, J.
1971. Sampling and distribution of animals in submerged vegetation. Věstník Československ. Společ. Zool. 35:209-21.

KRAUSE, A.
1977. On the effect of marginal tree rows with respect to the management of small lowland streams. Aquat. Bot. 3:185-92.

KRECKER, F. H.
1939. A comparative study of the animal population of certain submerged aquatic plants. Ecology 20:553-62.

KUNII, H.
1982. Life cycle and growth of *Potamogeton crispus* L. in a shallow pond, Ojaga-ike. Bot. Mag. Tokyo 95:109-24.

LAGLER, K. F.
1956. Freshwater fishery biology, 2nd ed. Wm. C. Brown, Dubuque, Iowa. 421 pp.

LANDERS, D. H.
1982. Effects of naturally senescing aquatic macrophytes on nutrient chemistry and chlorophyll *a* of surrounding waters. Limnol. Oceanogr. 27:428-39.

LEGENDRE, L., S. DEMERS, C. M. YENTSCH, AND C. S. YENTSCH
1983. The ^{14}C method: patterns of dark CO_2 fixation and DCMU correction to replace the dark bottle. Limnol. Oceanogr. 28:996-1003.

LIGHT, R. W., P. H. ADLER, AND D. E. ARNOLD
1983. Evaluation of gastric lavage for stomach analyses. North Am. J. Fish. Manage. 3:81-85.

LIKENS, G. E. AND J. J. GILBERT
1970. Notes on quantitative sampling of natural populations of planktonic rotifers. Limnol. Oceanogr. 15:816-20.

LIND, C. T. AND G. COTTAM
1969. The submerged aquatics of University Bay: a study in eutrophication. Am. Midl. Nat. 81:353-69.

LINDE, A. F.
1969. Techniques of wetland management. Wis. Dep. Nat. Resour. Res. Rep. No. 45. 156 pp.

LINDEMAN, R. L.
1942. The trophic-dynamic aspect of ecology. Ecology 23:399-418.

LUND, J. W., C. KIPLING, AND E. D. LECREN
1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimation by counting. Hydrobiologia 11:143-70.

LUX, F. E. AND L. L. SMITH, JR.
1960. Some factors influencing seasonal changes in angler catch in a Minnesota lake. Trans. Wis. Acad. Sci., Arts, and Lett. 89:67-79.

MACAN, T. T.
1970. Biological studies of the English lakes. Am. Elsevier Publ. Co., New York. 260 pp.

1977. Changes in the vegetation of a moorland fishpond in twenty-one years. J. Ecol. 65:95-106.

MACKENTHUN, K. M.
1946. A preliminary report of the age, growth and condition factor of southern Wisconsin fishes. Wis. Conserv. Dep. Div. Fish Manage. Invest. Rep. 574. 22 pp. (Unpubl. rep.).

MADSEN, T. V. AND E. WARNCKE
1983. Velocities of currents around and within submerged aquatic vegetation. Arch. Hydrobiol. 97:389-94.

MAGNIN, E.
1977. Écologie des eaux douces du territoire de la Baie James. Soc. Énergie Baie James, Montréal, Can. 454 pp. (1980 errata).

MAYHEW, J.
1956. The bluegill *Lepomis macrochirus* (Rafinesque) in West Okoboji Lake, Iowa. Iowa Acad. Sci. 63:705-13.

MCCAFFERTY, W. P.
1981. Aquatic entomology. Sci. Books. Int., Boston, Mass. 448 pp.

MCCORMICK, E. M.
1940. A study of the food of some Reelfoot Lake fishes. J. Tenn. Acad. Sci. 15:64-75.

McLachlan, A. J.
1969. The effect of aquatic macrophytes on the variety and abundance of benthic fauna in a newly created lake in the tropics (Lake Kariba). Arch. Hydrobiol. 66:212-31.

Megard, R. O.
1967. Three new species of *Alona* (Cladocera, Chydoridae) from the United States. Int. Revue ges. Hydrobiol. 52:37-50.

Merritt, R. W. and K. W. Cummins, eds.
1984. An introduction to the aquatic insects of North America, 2nd ed. Kendall/Hunt Publ. Co., Dubuque, Iowa. 722 pp.

Misra, R. D.
1938. Edaphic factors in the distribution of aquatic plants in the English lakes. J. Ecol. 26:411-51.

Mittelbach, G. G.
1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology 65:499-513.

Modlin, R. F.
1970. Aquatic plant survey of Milwaukee River watershed lakes. Wis. Dep. Nat. Resour. Res. Rep. No. 52. 45 pp.

Morgan, G. D.
1951. The life history of the bluegill sunfish, *Lepomis macrochirus*, of Buckeye Lake (Ohio). Denison Univ. J. Sci. Lab. Bull. 42:21-59.

Mrachek, R. J.
1966. Macroscopic invertebrates on the higher aquatic plants at Clear Lake, Iowa. Iowa Acad. Sci. 73:168-77.

Nalepa, T. F. and A. Robertson
1981. Screen mesh size affects estimates of macro- and meio-benthos abundance and biomass in the Great Lakes. Can. J. Fish. Aquat. Sci. 38:1027-34.

Nelson, M. N. and A. D. Hasler
1942. The growth, food, distribution and relative abundance of the fishes of Lake Geneva, Wisconsin, in 1941. Trans. Wis. Acad. Sci., Arts, and Lett. 34:137-48.

Nichols, S. A.
1974. Mechanical and habitat manipulation for aquatic plant management: a review of techniques. Wis. Dep. Nat. Resour. Tech. Bull. No. 77. 34 pp.
1975. The impact of overwinter drawdown on the aquatic vegetation of the Chippewa Flowage, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Lett. 63:176-86.

Nicholson, S. A.
1981. Changes in submersed macrophytes in Chautauqua Lake, 1937-1975. Freshw. Biol. 11:523-30.

Nuttall, P. M. and C. H. Fernando
1971. A guide to the identification of the freshwater Ostracoda with a provisional key to the species. Univ. Waterloo Biol. Ser. No. 1. 33 pp.

O'Donnell, D. J.
1940. Species of fish. Wis. Conserv. Dep. Fish Manage. Invest. Rep. 141. 3 pp. (unpubl. rep.).

Pace, M. L. and J. D. Orcutt, Jr.
1981. The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. Limnol. Oceanogr. 26:822-30.

Parker, R. A.
1958. Some effects of thinning on a population of fishes. Ecology 39:304-17.

Parks, C. E.
1949. Investigations of Indiana lakes and streams. 4. The summer food of some game fishes of Winona Lake. Invest. Ind. Lakes Streams 3:225-45.

Patrick, R. and C. W. Reimer
1966. The diatoms of the United States exclusive of Alaska and Hawaii. Acad. Nat. Sci. Philadelphia, Pa. Monogr. 13. Vol. 1, Part 1. 688 pp.
1975. The diatoms of the United States exclusive of Alaska and Hawaii. Acad. Nat. Sci. Philadelphia, Pa. Monogr. 13. Vol. 1, Part 2. 212 pp.

Pearsall, W. H.
1920. The aquatic vegetation of the English lakes. J. Ecol. 8:163-201.

Pearse, A. S.
1918. The food of the shore fishes of certain Wisconsin lakes. U.S. Bur. Fish. Bull. 35:245-92.
1921*a*. The distribution and food of the fishes of three Wisconsin lakes in summer. Univ. Wis. Stud. Sci. 3:1-61.
1921*b*. Distribution and food of the fishes of Green Lake, Wisconsin, in summer. U.S. Bur. Fish. Bull. 37:253-72.

Pennak, R. W.
1978. Fresh-water invertebrates of the United States. 2nd edition. Wiley-Interscience, John Wiley and Sons, New York. 803 pp.

Petersen, J. L. and W. Hilsenhoff
1972. The role of aquatic insects in the transfer of energy and nutrients through and out of Lake Wingra: a progress report. East. Deciduous For. Biome. Univ. Wis., Madison. Memo Rep. 72-57. 16 pp. (unpubl. rep.).

Peterson, B. J.
1980. Aquatic primary productivity and the $^{14}C-CO_2$ method: a history of the productivity problem. Ann. Rev. Ecol. Syst. 11:359-85.

Pielou, E. C.
1975. Ecological diversity. Wiley-Interscience, John Wiley and Sons, New York. 165 pp.

Pokrovskaya, T. N.
1983. Eutrophication of the macrophyte overgrown lakes. Hydrobiol. J. 19(3):12-18.

Pope, G. F., J. C. H. Carter, and G. Power
1973. The influence of fish on the distribution of *Chaoborus* spp. (Diptera) and density of larvae in the Matamek River system, Québec. Trans. Am. Fish. Soc. 102:707-14.

Prescott, G. W.
1962. Algae of the western Great Lakes, with an illustrated key to the genera of desmids and freshwater diatoms, rev. ed. Wm. C. Brown, Dubuque, Iowa. 977 pp.

Regier, H. A.
1962. Validation of the scale method for estimating age and growth of bluegills. Trans. Am. Fish. Soc. 91:362-74.
1963. Ecology and management of largemouth bass and bluegills in farm ponds in New York. N.Y. Fish and Game J. 10:1-89.

Reighard, J.
1913. An ecological reconnoissance of the fishes of Douglas Lake, Cheboygan County, Michigan, in midsummer. U.S. Bur. Fish. Bull. 33:215-49.

Rice, L. A.
1941. The food of six Reelfoot Lake fishes in 1940. J. Tenn. Acad. Sci. 16:22-26.

Rich, P. H., R. G. Wetzel, and N. Van Thuy
1971. Distribution, production and role of aquatic macrophytes in a southern Michigan marl lake. Freshwater Biol. 1:3-21.

Richards, P. W.
1966. The tropical rain forest: an ecological study. Univ. Press, Cambridge, England. 450 pp.

Richardson, F. B.
1974. Potential macrophyte production and management strategies for LaFarge Lake. pp. 211-49 *in* Environ. Anal. of the Kickapoo River impoundment. Cent. Biota. Syst. Inst. Environ. Stud. Univ. Wis., Madison. Rep. 28. 288 pp.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191. 382 pp.

Rickett, H. W.
1924. A quantitative study of the larger aquatic plants of Green Lake, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Lett. 22:381-414.

Rosine, W. N.
1955. The distribution of invertebrates on submerged aquatic plant surfaces in Muskee Lake, Colorado. Ecology 36:308-14.

Roszman, F. D.
1935. The age, rate of growth and the food of five species of game fish in Lake Erie. Ohio State Univ., Columbus. MS Thesis. 31 pp.

Roth, J. C.
1968. Benthic and limnetic distribution of three *Chaoborus* species in a southern Michigan lake (Diptera, Chaoboridae). Limnol. Oceanogr. 13:242-49.

ROTT, E.
1981. Some results from phytoplankton counting intercalibrations. Schweiz. Z. Hydrol. 43:34-62.

RYAN, T. A., JR., B. L. JOINER, AND B. F. RYAN
1981. Minitab reference manual. Stat. Dep. Pa. State Univ., Univ. Park, Pa. 154 pp.

SADZIKOWSKI, M. R. AND D. C. WALLACE
1976. A comparison of the food habits of size classes of three sunfishes (*Lepomis macrochirus* Rafinesque, *L. gibbosus* (Linnaeus) and *L. cyanellus* Rafinesque). Am. Midl. Nat. 95:220-25.

SAETHER, O. A.
1979. Chironomid communities as water quality indicators. Holarct. Ecol. 2:65-74.

SASTROUTOMO, S. S., I. IKUSIMA, M. NUMATA, AND S. ILIZUMI
1979. The importance of turions in the propagation of pondweed (*Potamogeton crispus* L.). Ecol. Rev. 19:75-88.

SCHIEMER, F.
1979. Submerged macrophytes in the open lake. Distribution pattern, production and long term changes. pp. 235-50 *in* H. Löffler, ed. Neusiedlersee: the limnology of a shallow lake in central Europe. Monogr. Biol. 37. W. Junk, the Hague.

SCHIEMER, F., H. LÖFFLER, AND H. DOLLFUSS
1969. The benthic communities of Neusiedlersee (Austria). Verh. Int. Verein. Limnol. 17:201-08.

SCHIEMER, F. AND M. PROSSER
1976. Distribution and biomass of submerged macrophytes in Neusiedlersee. Aquat. Bot. 2:289-307.

SCHLOEMER, C. L.
1939. The age and rate of growth of the bluegill *Helioperca machrochira* (Rafinesque). Univ. Wis., Madison. PhD Thesis. 113 pp.

SCHOENER, T. W.
1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408-18.

SCULTHORPE, C. D.
1967. The biology of aquatic vascular plants. Edward Arnold, London. 610 pp.

SEABURG, K. G.
1957. A stomach sampler for live fish. Prog. Fish-Cult. 19:137-39.

SEABURG, K. G. AND J. B. MOYLE
1964. Feeding habits, digestive rates, and growth of some Minnesota warmwater fishes. Trans. Am. Fish. Soc. 93:269-85.

SERNS, S. L. AND K. STRAWN
1975. Age and growth of bluegill, *Lepomis macrochirus*, in two heated Texas reservoirs. Trans. Am. Fish. Soc. 104:506-12.

SHANNON, C. E. AND W. WEAVER
1949. The mathematical theory of communication. Univ. Ill. Press, Urbana, Ill. 117 pp.

SHAW, S. P. AND C. G. FREDINE
1956. Wetlands of the United States. Their extent and their value to waterfowl and other wildlife. U.S. Fish Wildl. Serv. Circ. 39. 67 pp. (1971 printing).

SKUJA, H.
1948. Taxonomie des phytoplanktons einiger seen in Uppland. Schweden. Bot. Inst. Uppsala, Schweden. Symb. Bot. Upsal. 9(3):1-399 + tafeln.

SMART, M. M.
1980. Annual changes of nitrogen and phosphorus in two aquatic macrophytes (*Nymphaea tuberosa* and *Ceratophyllum demersum*). Hydrobiologia 70:31-35.

SMITH, G. M.
1950. The fresh-water algae of the United States, 2nd ed. McGraw-Hill, New York. 719 pp.

SMITH, K. AND C. H. FERNANDO
1978. A guide to the freshwater calanoid and cyclopoid copepod Crustacea of Ontario. Univ. Waterloo Biol. Ser. 18. 74 pp.

SMITH, S. H.
1954. Method of producing plastic impressions of fish scales without using heat. Prog. Fish-Cult. 16:75-78.

SNOW, H.
1969. Comparative growth of eight species of fish in thirteen northern Wisconsin lakes. Wis. Dep. Nat. Resour. Res. Rep. No. 46. 23 pp.

SPENCE, D. H. N.
1982. The zonation of plants in freshwater lakes. Ecol. Rev. 12:37-125.

SPRUGEL, G., JR.
1953. Growth of bluegills in a new lake, with particular references to false annuli. Trans. Am. Fish. Soc. 83:58-75.

STEMBERGER, R. S.
1979. A guide to rotifers of the Laurentian Great Lakes. U.S. Environ. Prot. Agency Rep. 600/4-79-021. 186 pp.

STRAUSS, R. E.
1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Trans. Am. Fish. Soc. 108:344-52.

STUNTZ, W. E.
1975. Habitat selection and growth of bluegills. Univ. Wis., Madison. PhD Thesis. 125 pp.

SWINDALE, D. N. AND J. T. CURTIS
1957. Phytosociology of the larger submerged plants in Wisconsin lakes. Ecology 38:397-408.

SWINGLE, H. S.
1950. Relationships and dynamics of balanced and unbalanced fish populations. Ala. Polytech. Inst. Agric. Exp. Stn. Bull. 274. 73 pp.

TARJAN, A. C., R. P. ESSER, AND S. L. CHANG
1977. An illustrated key to nematodes found in fresh water. J. Water Poll. Control Fed. 49:2318-37.

TE, G. A.
1975. Michigan Physidae, with systematic notes on *Physella* and *Physodon* (Basommatophora: Pulmonata). Malacol. Rev. 8:7-30.

TEBO, L. B., JR.
1955. Bottom fauna of a shallow eutrophic lake, Lizard Lake, Pocahontas County, Iowa. Am. Midl. Nat. 54:89-103.

TESCH, F. W.
1968. Age and growth. pp. 93-123 *in* W. E. Ricker, ed. Methods for assessment of fish production in fresh waters. Int. Biol. Program. Blackwell Sci. Publ., Oxford, England. Handbook 3. 313 pp.

TORKE, B. G.
1974. An illustrated guide to the identification of the planktonic Crustacea of Lake Michigan with notes on their ecology. Univ. Wis. Milwaukee Spec. Rep. 17. 42 pp.

1975. A key to the calanoid Copepoda of Wisconsin. Ball State Univ., Muncie, Ind. 4 pp. (unpubl. rep.).

1976. A key to the identification of the cyclopoid copepods of Wisconsin, with notes on their distribution and ecology. Wis. Dep. Nat. Resour. Res. Rep. No. 88. 16 pp.

U.S. ENVIRONMENTAL PROTECTION AGENCY
1979. Methods for chemical analysis of water and wastes, 2nd ed. U.S. Environ. Prot. Agency Rep. 600/4-79-020. 465 pp.

VERHOEVEN, J. T. A., R. P. W. M. JACOBS, AND W. VAN VIERSSEN
1982. Life-strategies of aquatic plants: some critical notes and recommendations for further research. pp. 158-64 *in* J. J. Symoens, S. S. Hooper, and P. Compère, eds. Studies on aquatic vascular plants. Roy. Bot. Soc. Belgium. Brussels, Belgium.

VOIGT, M.
1956. Rotatoria. Die Rädertiere Mitteleuropas. Gerbrüder Borntraeger. Berlin. Tafelband II. 115 pp.

VOIGTS, D. K.
1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. Am. Midl. Nat. 95:313-22.

VOLLENWEIDER, R. A., ED.
1969. A manual on methods for measuring primary productivity in aquatic environments. Int. Biol. Program. Blackwell Sci. Publ., Oxford, England. Handbook 12. 213 pp.

VOSS, E. G.
1972. Michigan flora. Part I. Gymnosperms and monocots. Cranbrook Inst. Sci. Bull. 55. 488 pp.

WATSON, S. AND J. KALFF
1981. Relationships between nannoplankton and lake trophic status. Can. J. Fish. Aquat. Sci. 38:960-67.

WEBB. D. W. AND W. U. BRIGHAM
1982. Aquatic Diptera. pp. 11.1-11.111 *in* A. R. Brigham, W. U. Brigham, and A. Gnilka, eds. Aquatic insects and oligochaetes of North and South Carolina. Midwest Aquat. Enterprises, Mahomet, Ill. 837 pp.

WEBER, C. I.
1971. A guide to the common diatoms at water pollution surveillance system stations. U.S. Environ. Prot. Agency, Cincinnati, Ohio. 98 pp.
1973. Biological field and laboratory methods for measuring the quality of surface waters and effluents. U.S. Environ. Prot. Agency Rep. 670/4-73-001.

WEBER, J. A.
1972. The importance of turions in the propagation of *Myriophyllum exalbescens* (Haloragidaceae) in Douglas Lake, Michigan. Mich. Bot. 11:115-21.

WELCH, P. S.
1948. Limnological methods. McGraw-Hill Book Co., New York. 381 pp.

WERNER, E. E., G. G. MITTELBACH, AND D. J. HALL
1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. Ecology 62:116-25.

WERNER, R. G.
1969. Ecology of limnetic bluegill (*Lepomis macrochirus*) fry in Crane Lake, Indiana. Am. Midl. Nat. 81:164-81.

WETZEL, R. G.
1983. Limnology, 2nd ed. CBS (Saunders) Coll. Publ. Co., Philadelphia, Pa. 767 pp.

WIGGINS, G. B.
1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. Toronto Press, Toronto, Ont. 401 pp.

WILE, I., G. HITCHIN, AND G. BEGGS
1979. Impact of mechanical harvesting on Chemung Lake. pp. 145-59 *in* J. E. Breck, R. T. Prentki, and O. L. Loucks, eds. Aquatic plants, lake management, and ecosystem consequences of lake harvesting. Univ. Wis., Madison. Cent. Biota. Syst. Inst. Environ. Stud. 435 pp.

WILKINSON, R. E.
1963. Effects of light intensity and temperature on the growth of water stargrass, coontail, and duckweed. Weeds 11:287-90.

WILLIAMS, D. D. AND N. E. WILLIAMS
1974. A counterstaining technique for use in sorting benthic samples. Limnol. Oceanogr. 19:152-53.

WILSON, L.
1941. The larger aquatic vegetation of Trout Lake, Vilas County, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Lett. 33:135-46.

WINDELL, J. T.
1967. Rates of digestion in fishes. pp. 151-73 *in* S. D. Gerking, ed. The biological basis of freshwater fish production. John Wiley and Sons, New York. 495 pp.

WINTERRINGER, G. S. AND A. C. LOPINOT
1966. Aquatic plants of Illinois. Ill. Dep. Registrat. and Educ., State Museum Div., and Dep. Conserv. Div. Fish. Pop. Sci. Ser. Vol. 6. 142 pp.

WISNIEWSKI, R. J. AND K. DUSOGE
1983. Ecological characteristics of lakes in north-eastern Poland versus their trophic gradient. Ekol Pol. 31:429-57.

WOOD, R. D.
1967. Charophytes of North America. A guide to the species of Charophyta of North America, Central America, and the West Indies. Univ. Rhode Island Bookstore, Kingston, R.I. 72 pp.

YEO, R. R.
1957. Life history of sago pondweed. Weeds 13:314-21.
1966. Yields of propagules of certain aquatic plants I. Weeds 14:110-13.

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I dedicate this Bulletin to my two partners, Vera and Legne, who alone stood by me when skies darkened.

ACKNOWLEDGMENTS

My thanks to nearly 75 field and laboratory assistants, reviewers, professional taxonomists, and other support staff. Critical reviews of the project proposal, the three progress reports, or Technical Bulletin manuscript came from Warren C. Churchill, Russell C. Dunst, Douglas R. Knauer, Eugene L. Lange, Richard C. Lathrop, David W. Marshall, Larry L. Maltbey, Stanley A. Nichols, Roy A. Stein, Donald R. Thompson, C. William Threinen, Gene J. Van Dyke, and Thomas L. Wirth. Further guidance was given by John W. Mason and S. Galen Smith. Eugene L. Lange and Michael D. Staggs advised on data analysis.

Tackling the field work and converting piles of samples to data sheets required teams of dedicated workers. Special thanks are due Paul J. Garrison and Richard P. Narf for guiding the algae and benthos analysis teams. Randall C. Wildman analyzed much of the benthos and fish stomachs, while setting high standards in all his work. My other superb "bug pickers" were Donald M. Bush, Don J. Conklin, Jr., Valerie Maniglièr, and Leanne J. Mumpy. Much praise for mapping and weighing macrophytes goes to Brian J. Andraski, MaryJo E. Moubry, Anne E. Tews, and Roseanne T. Wallander. Repair of the boom shocker used after June 1978 fell to Gregory I. Quinn and Gerald D. Wegner, who caught the fishes on most of the fall surveys. My thanks to Michael G. Burns and Shawn L. Johnson for gutting fishes, Robert E. Last and Pamela K. Montz for counting phytoplankton, and Richard L. Anderson for building sampling gear. Donald M. Bush and Wendell J. Wojner drilled over 120 ice holes enabling Eugene W. Eaton to draw a detailed lake map. Deirdre A. Berner, Jeffery M. Hager, Mary E. Hammel, Ann B. Hodges, Ann Marie Journey, Richard A. Lillie, and Robert G. Masnado assisted with data analysis for field work.

The project depended on support facilities or special services. David G. Armstrong loaned a scintillation counter for measuring productivity. Robert R. Badeau and Gerald G. Chipman periodically calibrated the light meter. George T. Bowman and Bob A. Schuknecht coordinated water analyses at the State Laboratory of Hygiene. Richard I. Purin and staff offered the facilities at Governor Dodge State Park. Louis E. Weston faithfully sent the 10-day weather reports from Dodgeville. Don M. Fago loaned the boom shocker used in 1977 and William J. Ryan made needed repairs to it. Herbert W. Wilson, Jr. came through with hurried requests for supplies or vehicles. The Nevin Library staff of Lois A. Komai, Alison Schmitz, and Rose B. Smith greatly assisted my literature search and retrievals.

The identity of troublesome taxa was checked by many authorities. Paul J. Garrison, Linda K. Graham, and Daniel E. Wujek identified some phytoplankton and bacteria. Russell C. Dunst, Stanley A. Nichols, Robert H. Read, and S. Galen Smith confirmed the macrophyte species. Rotifers were identified by Richard S. Stemberger; ostracods by L. Dennis Delorme; cladocerans and copepods by Stanley I. Dodson, Vladimír Kořínek, Steven E. Mace, Robert O. Megard, and Byron G. Torke; *Chaoborus* species by Edwin F. Cook; and Chironomidae by William L. Hilsenhoff and Richard P. Narf. Troublesome fish scales were aged by Clifford L. Brynildson or Howard E. Snow.

Doel and Marvin Halverson kindly shared their recollections of the origin and early condition of their father's pond.

My parting thanks go to Ruth L. Hine for patiently keeping me on track and expertly bundling this opus.

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Sandy Engel earned his PhD in 1972 at the University of Wisconsin-Madison. His graduate research dealt with interactions among zooplankton, cisco, yellow perch, and coho salmon on Pallette Lake, Vilas County. After teaching environmental courses at a Michigan university, he joined the DNR's Bureau of Research in 1976. Besides his Halverson Lake studies, Sandy has completed work on Marion Millpond and Cox Hollow Lake. His recent publications deal with various physical methods of controlling lake vegetation.

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