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MINERAL DYNAMICS OF THE SUBMERSED MACROPHYTE, MYRIOPHYLLUM

HETEROPHYLLUM, AND THE COMPETITIVE INTERACTIONS FOR NUTRIENTS

BETWEEN M. HETEROPHYLLUM, PHYTOPLANKTON AND THE SEDIMENTS IN

LITTORAL WATERS

By

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and

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TECHNICAL COMPLETION REPORT

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ABSTRACT

     Myriophyllum heterophyllum is a nuisance, submersed hydrophyte in
New Hampshire. First observed in Lake Winnipesaukee, New Hampshire
during the 1960's, the plant infested over 22 miles of the lake's shore-
line by 1980. Circumstantial evidence suggests that M. heterophyllum
was accidently introduced to New Hampshire by trailered boats from Southern
New England. Lake Winnipesaukee now acts as a source for new infestations
elsewhere in the region. Physiological and ecological data that relate
to the recent success of this species in the state are reviewed.

     The emergent floral stem, apex, sub-apex, mid-stem, lower stem,
and roots of M. heterophyllum were analyzed for ash, P, Na, K, Ca, Mg, Fe,
Mn, Zn, Cu, and Pb from June 1979 through July 1980 at two sites in Lake
Winnipesaukee. The plant structures differed significantly in mineral
content, but seasonal pulses for each mineral were usually in synchrony
between the different structures sampled. Na and K were the dominant
minerals, with the exception of Ca in the floral spike and Fe in the
roots. Na concentrations were highest in the stem. It is speculated
that the Na and K levels in the stem may develop sufficient negative
osmotic potential in the stem to facilitate the movement of water and
minerals from the roots to the stem. The structural role and slow
mobilization in the phloem of Ca explain its high concentration in the
floral stem. Root losses of oxygen and oxidizing enzymes cause the
formation of a sheath of precipitated iron on the roots. M. heterophyllum's
mineral requirements are not fulfilled by previous storage or luxury
uptake. Rather, the data suggest that M. heterophyllum immediately mobilizes
minerals from nutrient rich sediments to meet nutrient needs.

     From 1977-1979 the competitive interactions between M. heterophyllum,
phytoplankton and sediments in the littoral zone of Lake Winnipesaukee
were examined. Nutrient additions were made to in situ enclosures with
(a) littoral water only, (b) littoral water and rooted M. heterophyllum,
(c) littoral waters and sediments, and (d) littoral water, sediments and
rooted M. heterophyllum. Changes in the littoral zone of Front Bay, Lake
Winnipesaukee, before and after continuous nutrient additions from nutrient

rich sewage treatment plant effluent were also monitored. The results suggest that nutrient levels in the water determine submersed macrophyte versus phytoplankton dominance in the littoral zone and the littoral sediments' capacity to sorb phosphorus is a critical factor in regulating nutrient availability in the water. Data on the seasonal changes in phytoplankton and water chemistry in littoral waters harboring dense growths of M. heterophyllum and the impact of herbicide treatment of aquatic weeds are also presented.

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(Myriophyllum heterophyllum Michx.) IN NEW HAMPSHIRE

Introduction

The submersed aquatic angiosperm, Myriophyllum heterophyllum Michx.,
of the Haloragaceae family and commonly known as water milfoil, is a
recent immigrant to northern New England. Within the genus Myriophyllum,
there are seven species which are indigenous to northern New England:
M. alterniflorum, M. exalbscens, M. Farwelli, M. humile, M. pinnatum,
M. verticillatum and M. tenellum (Fassett 1969). Eurasian water milfoil,
M. spicatum, is another exotic that has successfully colonized some of
the hard-water lakes and ponds of New England during this century, although
it has not been reported from New Hampshire. Both M. heterophyllum and
M. spicatum are nuisance aquatic weeds in New England.

Major infestations of M. heterophyllum in New Hampshire were first
observed during the 1960's in the state's largest waterbody, Lake Winnipe-
saukee. During the 1970's the species spread to several lakes and ponds
adjacent to Lake Winnipesaukee. The dense, monospecific growths of the
water milfoil frequently reach the surface, where they impair boat
navigation and swimming, tangle fish lines and displace native aquatic
flora. Once established, eradication of this species is most difficult.
Attempts to control M. heterophyllum in Lake Winnipesaukee (Fig. 1) have
included aquatic weed harvesting in Smith Cove, Salmon Meadow Cove, Lees
Mill and Front Bay; the use of benthic barriers (Mayer 1978, Perkins et al.
1980) in Front and Alton Bay; and herbicide treatment in Crescent Lake,
and Alton Bay, Salmon Meadow Cove, Ash Cove and the upper reaches of
Moultonboro Bay in Lake Winnipesaukee. These management techniques are
expensive, and require yearly maintenance of applications to inhibit regrowth.
Lake Winnipesaukee's chemical treatment programs used the controversial
herbicide, Silvex (2,4,5-trichlorophenoxypropionic acid, or 2,4,5-TP),
until it was banned by the federal government in 1978. The purpose of
this section is to document the distribution of M. heterophyllum in New
Hampshire, and review the existing physiological and ecological data that
relate to the recent success of this species in the state.

FIGURE **1.** 1980 DISTRIBUTION OF MYRIOPHYLLUM HETEROPHYLLUM IN THE LAKES REGION, NEW HAMPSHIRE

Site Number	Site Location	Ha	Acres	Site Number	Site Location	Ha	Acres
1	Basin (Tuftonboro)	2.8	7	30	Guay Island to Marker 52 (Moultonboro)	2.0	5
2	Edmunds Cove (Wolfeboro)	0.1	0.3	31	Marker 52 to Hanson Cove (Moultonboro)	4.0	10
3	Front Bay (Wolfeboro)	12.1	30	32	Greens Basin (Moultonboro)	8.9	22
4	Mink Brook (Wolfeboro)	0.04	0.1	33	Badger Island (Moultonboro)	6.1	15
5	Springfield Point (Wolfeboro)	0.2	0.5	34	Evergreen Island (Moultonboro)	8.1	20
6	Roberts Cove (Alton)	0.3	0.7	35	Lees Mill (Moultonboro)	8.1	20
7	Alton Bay (Alton)	1.2	3	36	Balmoral to Ganzy Island (Moultonboro)	7.3	18
8	Parkers Marina (Alton)	0.9	2.3	37	Ganzy Island to Hemlock Point (Moultonboro)	3.6	9
9	Merrymeeting River (Alton)	0.8	2	38	Hemlock Cove (Moultonboro)	0.8	2
10	Back Bay (Alton)	0.4	1	39	Black Point – Areys Marina (Moultonboro)	0.4	1
11	Minge Cove Marina (Alton)	0.4	1	40	Clarks Landing (Moultonboro)	0.1	0.3
12	Smalls Cove (Alton)	1.6	4	41	Melvin Village (Melvin Village)	0.1	0.2
13-15	Smith Cove (Gilford)	6.1	15	42	Melvin Village Marina (Melvin Village)	0.1	0.2
16	Gilford Marina (Gilford)	1.6	4	43	Copps Pond Outlet (Melvin Village)	0.4	0.9
17	Silver Sands Marina (Gilford)	0.4	1	44	20 Mile Bay (Tuftonboro)	0.04	0.1
18	Pickerel Cove (Laconia)	0.2	0.5	45	19 Mile Bay (Tuftonboro)	0.3	0.8
19	Meredith Bay (Meredith)	0.04	0.1	46	Lees Pond (Moultonboro)	0.5	1.2
20	Meredith Neck (Meredith)	0.1	0.3	47	Lake Wentworth – Mast Landing (Wolfeboro)	0.4	1
21	Fish Cove (Meredith)	0.4	1				
22	Blackeye Cove (Center Harbor)	0.4	1				
23	Black Cat Island (Center Harbor)	0.1	0.3				
24	Ash Cove (Moultonboro)	2.0	5				
25	Salmon Meadow Cove (Moultonboro)	1.1	2.7				
26	Harilla Landing (Moultonboro)	0.2	0.5				
27	Langdon Cove (Moultonboro)	0.04	0.1				
28	Clark Point (Moultonboro)	0.4	1				
29	Guay Island to Deepwood Lodge (Moultonboro)	2.4	6		TOTAL	87.6	217.1
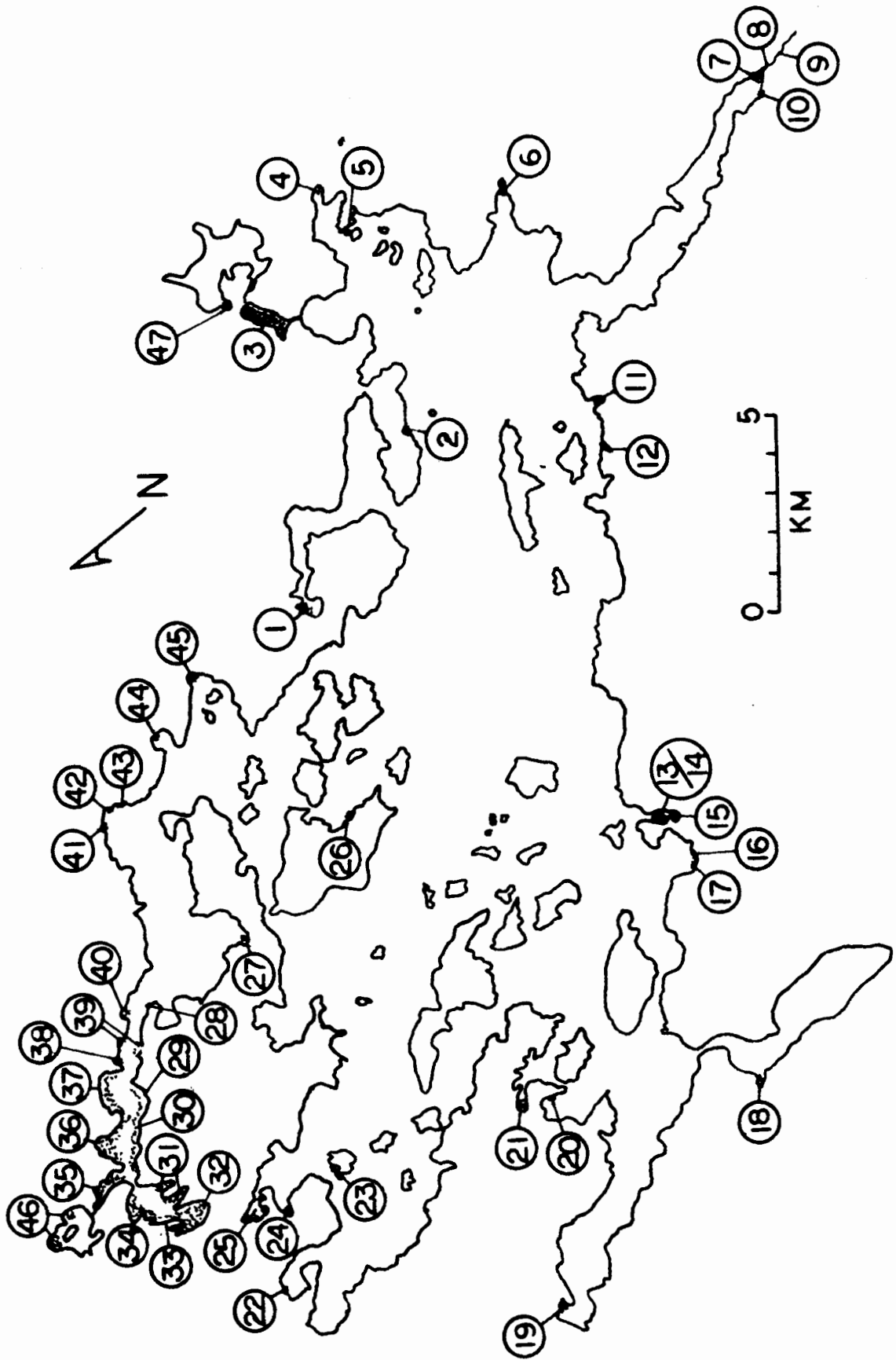
Description of the Plant

Myriophyllum heterophyllum exhibits a heterophyllous morphology (Fig. 2). The long, flexible stems may reach 3.5 m in length and are attached to a fibrous root system. There are three leaf types, with submersed leaves being the predominant form. Submersed leaves are pinnately compound with 4 to 10 pairs of leaflets and have an irregular pattern of multicellular trichomes. Stomates are absent (England and Tolbert 1964). The stem becomes leafless toward the rooted base, due to release or decay of leaves. Flowering plants develop an emergent stem, bearing transitional and aerial leaves. The emergent stem commonly is S-shaped. The submersed stem bends at the surface, where it becomes enlarged, thickened and stiffened, and then points upward. The enlarged horizontal stem bears transitional leaves and provides sufficient ballast to keep the inflorescence in an upright position. The transitional leaves are pinnatisect with an entire margin and have trichomes and several stomata. Aerial leaves, called floral bracts (Fassett 1969), are simple, elliptical-to-ovate leaves with a serrulate margin. Stomata are abundant on both surfaces (England and Tolbert 1964). Flowering plants are monoecious, with the flowers in the axils of the floral bracts (Fig. 2). The pistillate flowers are basipetal to the staminate flowers. Aerial stems laying on the surface of the water after flowering were observed to frequently revert back to a submersed form. Adventitious roots are common on the submersed stems from mid-summer until spring.

Similar to many submersed hydrophytes, the xylem tissue is greatly reduced in M. heterophyllum. The phloem is not reduced, and a Casparian strip is still present in the endodermis of the roots (Sculthorpe 1967). Myriophyllum heterophyllum's well-developed lacunae system (Fig. 2) accounts for much of the plant's volume. The lacunae system, though interrupted by thin partitions, acts as an internal gas reservoir, capable of allowing diffusive exchange between the roots and shoots (Grace and Wetzel 1978).

Flowering spike

Whorl of leaves

X - section of Stem

epidermal cell

mesophyll cell

lacuna

endodermis

vascular strand
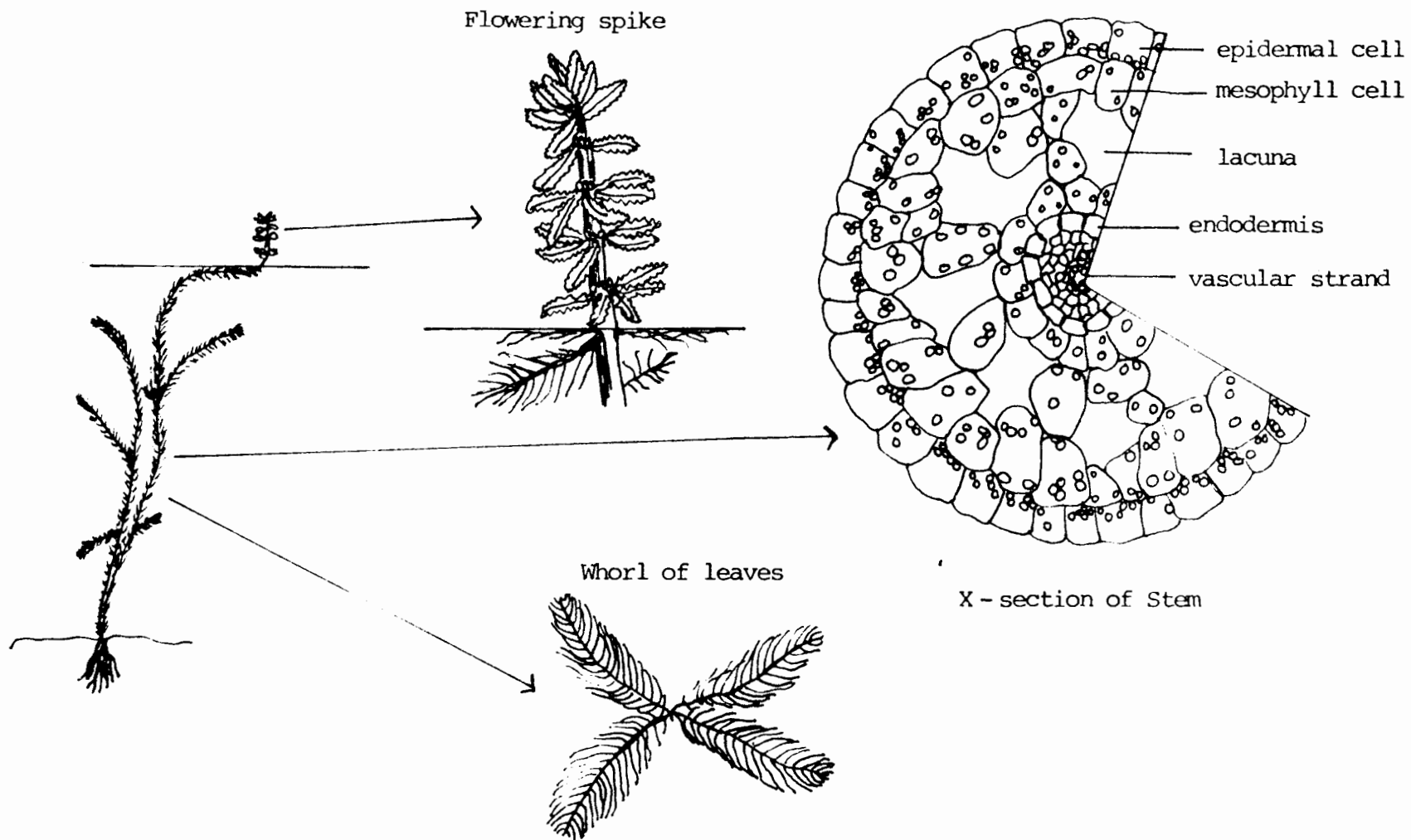
Figure 2. Habit of Myriophyllum heterophyllum

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Habitat

In New Hampshire, Myriophyllum heterophyllum appears to be habitat
specific. It generally occurs as mono-specific stands in water 0.5 to
5 m deep, primarily along the shores of lakes, ponds and sluggish rivers.
It rarely grows deeper, probably because of hydrostatic pressure and
light limitation (Grace and Wetzel 1978). Myriophyllum heterophyllum
successfully colonizes coves with gradually sloping shores which are
protected from extensive wind and wave turbulence. Such habitats have
fine, flocculent, muddy, silty, or silty-sandy sediments, with organic
concentrations of 1 to 38% (Penniman 1977). SCUBA obervations in Lake
Winnipesaukee from 1977 through 1979 suggest that viable vegetative
fragments of water milfoil cannot successfully root in coarse sand, cobble
or rocky substrata which are exposed to wave action.

Myriophyllum heterophyllum inhabits acidic water (pH 6-7), which are
relatively low in chloride (20 mg 1^{-1}) and dissolved ions (conductivity
10-100 μmho cm^{-1}, 20° C) (Beal 1977). Surface waters infested with
M. heterophyllum in New Hampshire have similar water chemistry.

Reproduction

Asexual reproduction is the primary means of reproduction for
Myriophyllum heterophyllum. Fragmentation occurs naturally by wave action
and by boat activities. The occurrence of free-floating fragments was
common throughout Lake Winnipesaukee during 1980, with the greatest
concentrations being downwind from infested areas. The fragments even-
tually become negatively buoyant and settle to the bottom. If they land
in quiescent coves, they will take root. The fibrous root system that
develops can give rise to many separate stems. The development of compact,
abortive leaf tissue, or turions, is common during late summer to autumn.
Apparently hormonal balance, influenced by environmental factors, determines
the onset of turion formation and subsequent development in this genus
(Amundsen and Brenkert 1978). Established plants also proliferate by
rhizomes which produce new clumps of stems. Invasion of suitable habitat
by vegetative propagation can occur rapidly, as exemplified by Front Bay
in Wolfeboro, NH. In 1977, M. heterophyllum populations were localized,

sparse, and flowering was not observed. By 1979 the entire 12 hectares
of this bay were infested.

In Lake Winnipesaukee, flowering by M. heterophyllum is common, but
specific information on the floral biology and seed viability is sparse.
Patten (1956) concludes that M. spicatum pollination may occur by both
anemophily and entomophily. Whether the plants are self-compatible is
unknown. After flowering in August, the emergent spikes float on the
water surface. Myriophyllum spicatum seeds are viable for at least seven
years (Davis et al. 1973) but seedling establishment appears to be a
critical stage in the life history (Patten 1956).

Both mallards (Anas platyrhynchos) and black ducks (Anas rubripes)
feed on M. heterophyllum floral stems in Lake Winnipesaukee. However,
they are not considered to be an important vector in dispersing the plant,
as most new infestations in the Lakes Region originated at boat launch
sites and marinas, suggesting that boats carrying vegetative fragments
are the primary vector.

Phenology

The yearly growth pattern of M. heterophyllum in Lake Winnipesaukee
can be divided into five phases.

Phase I: Late December to April. During this phase the water milfoil
is typically covered by a canopy of ice and snow. The plants are dormant
and commonly prostrate, particularly at locations subject to tributary flow.
During years of minimal snow fall and when the ice is transparent, a
situation that occurred during the unusually dry 1979-1980 winter, consider-
able upright biomass may be maintained throughout the winter. Apices on
upright stems are frequently frozen into the ice and broken free from the
parent stem. No appreciable elongation occurs during this phase.

Phase II: May to June. Following ice-out in late April, rapid
elongation occurs. Growth originates from short stems coming from the root-
stock and apices on old stems, both of which had formed during the late
summer. By late May, the submersed stems are within 1 m of the water surface.
Upon reaching the surface in mid-June, the stems grow along the surface to
form a dense canopy. Elongation rates up to 1.9 cm day^{-1} have been recorded

(Chagnon and Baker 1979). Plants growing deeper than 3 m rarely reach the surface.

Phase III: Late June to mid-August. Flowering begins in late June and continues into August. The fruit is set when the emergent, floral stems lose their rigidity and float on the surface in early August. Flowering does not occur at all sites or every year. After mid-July, elongation rates decrease (Chagnon and Baker 1979), but the density of the surface canopy may increase, because the lake level recedes by 20 to 50 cm. During July, leaves on the lower stem may slough off, particularly where a dense surface canopy has formed.

Phase IV: Late August to October. Emergent stems lose their rigidity, float on the surface and frequently break-free from the parent plant. New growth on floating emergent stems reverts back to a submersed leaf and stem morphology. Periphyton growth may become extensive. Elongation rates are much reduced during this phase. New compact stems develop at the base of the plants, and turions and adventitious roots grow on the main submersed stems. The surface canopy is thinned because of the sloughing-off of plant parts.

Phase V: November to December. The newer green stems remain upright. The older, dark and brittle stems that may contain turions, continue to break-off or settle to the bottom. Elongation ceases and the plant becomes dormant.

Standing Crop, Biomass and Productivity

Plant densities vary in areas infested by Myriophyllum heterophyllum from sparse to extensive coverage of the water column. Chagnon and Baker (1979) measured maximum densities of 40 plants m^{-2}. The estimated mid-summer biomass of M. heterophyllum excluding roots and rhizomes in Lake Winnipesaukee for 1.5 m high plants is 255 g dry wt m^{-2} (Table 1). Biomass values for M. spicatum generally range from 2--0400 g dry wt m^{-2} (Grace and Wetzel 1978), but this species is frequently covered by marl deposits which increase biomass measurements. Similarly, most standing crop biomass estimates for submersed macrophytes are less than 500 g dry wt m^{-2} (Wetzel 1975). Compared to emergent hydrophytes, these are low biomass values. The anomaly that M. heterophyllum has a relatively low

TABLE 1. ESTIMATED MID-SUMMER BIOMASS

OF <u>MYRIOPHYLLUM</u> <u>HETEROPHYLLUM</u>

IN LAKE WINNIPESAUKEE

Parameter	Value	Source
$\overline{X}$ above root dry wt	0.01 g per cm stem	Lees Mill Cove, Lake Winnipesaukee (Kimball, unpublished)
$\overline{X}$ stems per plant	10 stems per plant	Chagnon and Baker 1979
$\overline{X}$ density	17 plants per m^2	Chagnon and Baker 1979
Height	150 cm	- -

Above root dry wt biomass for 150 cm plants =

$$\frac{0.01 \text{ g}}{\text{cm stem}} \times \frac{10 \text{ stems}}{\text{plant}} \times \frac{17 \text{ plants}}{m^2} \times \frac{150 \text{ cm}}{\text{stem}} = 255 \text{ g per } m^2$$

above-ground biomass, yet physically occupies much of the water column is explained by the extensive air space or lacunal system, which can account for 18 to 43% of the total plant volume in $\underline{M}$. heterophyllum (Hartman and Brown 1967).

Productivity rates of $\underline{M}$. heterophyllum are unknown, but the mean growing season ranges for $\underline{M}$. spicatum are 0.3 to 3.0 g m^{-2} day^{-1} (Grace and Wetzel 1978).

Maximum photosynthetic rates for $\underline{M}$. spicatum occur at 0.8-0.9 m water depth in May, and 56% of the plants' productivity occurs in the top 100 cm of the water column. By August, a dense water milfoil canopy exists, and 57% of $\underline{M}$. spicatum's photosynthetic activity takes place in the top 20 cm of the water (Adams et al. 1974).

<div align="center">Physiology</div>

Photosynthesis in northern temperate softwater lakes has the possibility of CO_2 limitation, because of low total inorganic carbon availability. In dense canopies of water milfoil, conditions of high light levels at the surface also prevail. Though a C_4 carbon fixation pathway is potentially of adaptive value to aquatic plants in these environments, recent studies conclude that a true C_4 pathway in water milfoil is unlikely. However, Myriophyllum exhibits characteristics of both C_3 and C_4 plants. The predominant carboxylation enzyme is ribulose bisphosphate (RuBP) carboxylase, not phosphoenolpyruvate (PEP) carboxylase. The initial product of CO_2 fixation is 3-P-glycerate, and glycolate oxidase has been measured, as in C_3 plants (Stanley and Naylor 1972, 1973). Myriophyllum heterophyllum does not have the C_4 or Krantz anatomy, where the bundle sheath cells contain a few large starch containing chloroplasts. Rather, the main photosynthetic tissue is in the epidermis, which contains numerous small chloroplasts. An anatomical characteristic resembling the Krantz anatomy exists in the mesophyll cell chloroplasts, which are larger and contain considerable starch (Grace and Wetzel 1978, Hough and Wetzel 1977). Characteristics resembling C_4 plants in water milfoil are the low CO_2 compensation point and high temperature optimum (Stanley and Naylor 1972, 1973, Van et al. 1976). Factors that may contribute to the lower photorespiration rates in water milfoil, compared to C_3 plants, are functional differences

in the epidermal and mesophyll chloroplasts, an efficient recapture mechanism for respired carbon, removal of the soluble carbohydrates from solution in the cells (Amundsen and Brenkert 1978), lower glycolate oxidase activity (Van et al. 1976), the greater resistance of water to diffusion of CO_2, and the retardation of respired CO_2 loss by its storage in the gas lacunae (Wetzel 1975).

In areas of dense aquatic vegetation, most of the daily photosynthetic activity occurs during the early morning hours (Van et al. 1976), and photorespiration may increase during the day with increasing light intensities, and oxygen tension of photosynthetic origin, temperatures, and possibily decreasing CO_2 availability (Wetzel 1975). Photorespiration rates may also increase as the plants approach senescence or winter dormancy (Hough 1974).

Water milfoil uses free CO_2 as a source of carbon in photosynthesis, but has the ability to use bicarbonate. Photosynthesis in water milfoil was found to be independent of pH, and the ionic composition of the water, if free CO_2 was the carbon source. With bicarbonate ions as the source, photosynthesis was dependent on the ionic content of the water, because cations were absorbed to achieve charge balance (Steeman-Nielsen 1947). Another hypothesized carbon source is the conduction of carbon dioxide from the sediments into the root system and then upward through the lacunae into the leaves (Amundsen and Brenkert 1978).

The uptake of nutrients by water milfoil occurs through both the roots and shoots, but sediments are probably more important sources of nitrogen and phosphorus (Barko and Smart 1980). Submersed hydrophytes can not generate a transpirational pull to transport water solutes from root to shoot, and the mechanism of ion transport is yet to be conclusively demonstrated. When rooted in sediments, root hairs and a Casparian strip are present on the roots. The very thin cuticle and hydropoten are thought to be associated with ion absorption by the stem (Grace and Wetzel 1978).

Ecological Considerations

Myriophyllum heterophyllum grows from established root stocks straight to the surface, with relatively little branching to form a dense canopy of

photosynthetic tissue. In Lake Winnipesaukee, the plant effectively
shades-out competing native macrophytes. The competitive advantage for
this species is not totally explained by an exceptional growth rate.
Rather, the plant has an efficient means of dispersal, being able to
regenerate from relatively small fragments. Its morphology results in
a large increase in photosynthetic area, relative to its biomass produc-
tion, and a relatively large viable vegetative biomass overwinters and
holds space for the following year.

The rapid elongation rate of water milfoil reduces problems of
extensive periphyton growth on its surface. From May until mid-summer,
the plant creates new stem material faster than it can be colonized by
periphyton. As the elongation rate declines during late summer, epiphyte
coverage increases.

Though old water milfoil stems decay rapidly, no direct evidence of
herbivores feeding on submersed portions of the plant were observed by
SCUBA. Also, no insect parasites on Myriophyllum have been reported from
North America (Aiken et al. 1979). Insects and ducks were observed to
feed on water milfoil's emergent plant structures.

Invertebrates are abundant in the water milfoil stands and the
perimeters of water milfoil beds in Lake Winnipesaukee are frequented by
fishermen. Fyke net samples of game fish from water milfoil beds in Front
Bay, Wolfeboro (Brewster Academy ecology class data 1980), verify that
warm-water game fish are not adversely affected by water mifoil growth.

Range of the Plant

Myriophyllum heterophyllum is a native plant in North America,
occurring from the Plains states to the Atlantic coast, as well as Mexico
and eastern Canada (Fassett 1969, Martin and Uhler 1939, Muenscher 1944).
In northern New England its distribution appears to be both very recent
and disjunct. A review of specimens in the University of New Hampshire's
Herbarium, the Gray Herbarium at Harvard University, and the New England
Botanical Club Herbarium and local flora listings (Bean, unpubl., Blake
1959, Corbett unpubl., Dole 1937, Eaton 1974, Hoffman 1922, Jackson 1909,
Jesup 1891, Ogden et al. 1948, Palmatier 1952, Seymour 1969, State of

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Connecticut 1910) shows no specimens of M. heterophyllum collected in Maine, Vermont or New Hampshire prior to the 1970's. The species appears to have been established in Connecticut and south-central Massachusetts (Seymour 1969) prior to its spread into northern New England. The oldest New England specimen in these herbaria was reported to have escaped from a small pond and become naturalized in Bridgeport, Connecticut in 1932 (Harvard University Gray Herbarium Specimen #11.454). Circumstantial evidence indicates that M. heterophyllum colonized Lake Winnipesaukee in the 1960's, following completion of Interstate 93 from Boston to the Lakes Region, New Hampshire. Interstate 93 encouraged a rapid increase in the number of transient boats being trailered to Lake Winnipesaukee from M. heterophyllum infested surface waters in eastern Massachusetts. Myriophyllum heterophyllum's presence has been verified in Lake Winnipesaukee, Lake Wentworth, Lees Pond (Fig. 1) and Blackadar Pond in Alton, NH (Penniman, 1977). At both Lake Wentworth and Lees Pond, the initial site of infestation was a public boat launch. No reports of M. heterophyllum in Vermont exist, but Thompson Lake in Casco, Maine was recently infested at a public boat launch (D.L. Courtmanche, Maine Department of Environmental Conservation, pers. comm.)

It is hypothesized that boaters were the vectors in transporting M. heterophyllum to Lake Winnipesaukee from eastern Massachusetts and that trailered boats are now spreading water milfoil from Lake Winnipesaukee to other surface waters in the state. The following facts support this hypothesis.

1. The primary means of reproduction for water milfoil is vegetative propagation. A floating fragment is capable of developing into a new plant.

2. Boats traveling through waters infested with M. heterophyllum readily cut off and wrap strands of the plant on their propellers. Boat trailers, boat wells, and anchor ropes also easily catch and transport water milfoil strands.

3. British Columbia, which is experiencing serious problems with M. spicatum, conducted a survey of boat trailers and boats on their highways. A significant number of the boats and boat trailers leaving infested waters were found to be trans-

porting viable water milfoil fragments (Province of British Columbia 1980).

4. If waterfowl were the primary vector, many of New Hampshire's wetlands and ponds should be infested, because these waters are frequented by waterfowl. Infestation of these waters has not occurred.

Case Study on the Distribution of Myriophyllum heterophyllum in Lake Winnipesaukee

There have been three inventories of Myriophyllum heterophyllum's distribution in Lake Winnipesaukee. The first was a shoreline survey during 1975-1976 (Penniman 1977). Penniman noted that the entire lake was not surveyed. In August and September 1979, the NH Water Supply and Pollution Control Commission (inpubl.) undertook a cursory inventory of Lake Winnipesaukee, with the exception of Paugus Bay. Neither of these two inventories made an attempt to determine the surface area infested by M. heterophyllum. The following data represents the results of a third inventory of M. heterophyllum's distribution in Lake Winnipesaukee, during the summer of 1980.

The entire shorelines of Lake Winnipesaukee, Lake Wentworth and Lees Pond (Fig. 1) were circumnavigated by boat. All littoral waters with aquatic plants were observed using an underwater viewer and/or by snorkeling. Each location harboring M. heterophyllum was measured for the surface area of the infestation, the depth range of the plant, the type of substratum, and the shoreline usage. The surface area of each water milfoil infestation was determined by measuring the boundaries of the plant stand with a Rangematic 1000 range finder, or by defining the boundaries on a map and quantifying the area with a planimeter. Depths were measured with a weighted rope marked at 0.5 m intervals.

The location and surface area of all areas occupied by M. hetero- phyllum are illustrated in Figure 1. In 1980, Lake Winnipesaukee had 88 ha (217 acres) infested by M. heterophyllum. Many of these stands were long, narrow bands paralleling the shoreline. Approximately 22 miles of shoreline were infested, consequently the conflict between the

plant's growth and recreational usage of the shoreline had become very significant. The sites with the largest infestations were (a) Front Bay in Wolfeboro, 12 ha, (b) the mouth of the Merrymeeting River and south end of Alton Bay in Alton, 3 ha, (c) Smith Cove and the marinas in Saunders Bay in Gilford, 10 ha, (d) Ash Cove (herbicide-treated), Salmon Meadow Cove, and the north end of Moultonboro Bay in Moultonboro, 55 ha, and (e) the Basin in Tuftonboro, 3 ha. The most suitable habitat for this plant was in the upper reaches of Moultonboro Bay, where approximately 58% of the total area occupied by M. heterophyllum in Lake Winnipesaukee occurred.

Comparisons between the three surveys to determine the plant's rate of spread during the 1970's are not possible. The 1975-1976 and 1979 inventories provided only incomplete qualitative data. However, M. heterophyllum was expanding its distribution within Lake Winnipesaukee during the 1970's. Following September 1977, approximately 12 ha of Front Bay in Wolfeboro were infested within two years. Penniman (1977) reports that M. heterophyllum populations at Lees Mill, Roberts Cove Marina and Ostrands Marina in Smith Cove were sparse or nonexistent during 1975, but very extensive by late 1976. The size and density of water milfoil stands change yearly, because the environmental factors affecting growth rate are inconsistent from year to year.

It is evident from the 1980 survey that M. heterophyllum has not successfully colonized shorelines exposed to strong wind and wave action. The plant occupies secluded, calm waters with depths less than 5 meters. In Lake Winnipesaukee, the most preferred habitats are now colonized. Consequently, the rate at which new sites in Lake Winnipesaukee are invaded will probably decrease. Several small infestations may expand in the future, including those at Fish Cove (Meredith Bay) and Pickeral Cove (Paugus Bay).

During 1979 or 1980, M. heterophyllum was accidently introduced into Crescent-Wentworth Lake at Mast Landing (Fig. 1), and it had spread from the initial site by 1981. A 2,4-D granular herbicide treatment was made in 1981 to reduce the potential problem. The growth in Lees Pond has dispersed out from the public boat launch site and apparently stabilized.

The most serious problem for the surface waters of New Hampshire is that Lake Winnipesaukee will act as a source for spreading M. heterophyllum. Almost 50% of the public and marina boat launch sites on Lake Winnipesaukee are now infested with water milfoil growth (Table 2). Boats will continue to transport viable fragments from these launch sites to other surface waters as they did to Lake Wentworth and Lees Pond.

TABLE 2.   MARINA AND PUBLIC LAUNCH SITES INFESTED WITH WATER MILFOIL

	Number of Sites Infested		
Lake Winnipesaukee	Private Docks	Marina	Public Launch
Front Bay, Wolfeboro			1
Roberts Cove		1	
Alton Bay		1	1
Minge Cove		1	
Small Cove		1	
Smith Cove		3	
Saunders Bay		2	
Meredith Bay	1		
Long Island, Harilla's Landing		1	1
Lees Mill			1
Suissvale/Balmoral	2		1
Ambrose Cove		1	
Melvin Village	1	1	1
19 Mile Bay		1	

Other Waterbodies

Lees Pond			1
Crescent Lake, Mast Landing (Lake Wentworth)			1

II. SEASONAL VARIATIONS IN THE MINERAL CONTENT OF SIX STRUCTURES OF MYRIOPHYLLUM HETEROPHYLLUM MICHX.

Introduction

Characterisics of the hydrosoils, water and climate interact to determine the availability of minerals for uptake and utilization by submersed hydrophytes. The mineral content of aquatic plants is also influenced by the plants' need to maintain osmotic potential, seasonal changes in metabolic requirements, and the ontogenetic age of the plant. In addition, the sites of mineral uptake and mechanisms of transport in submersed hydrophytes differ considerably from those in terrestrial plants. The normal transport of ions in terrestrial plants is in the water flow of the xylem, from the root uptake site to the stem and leaves. In comparison, submersed hydrophytes have a greatly reduced xylem, transpiration is absent, and the vascular strands are condensed into a central cylinder (Sculthorpe 1967). The uptake sites in submersed hydrophytes for required minerals occur in the leaves (DeMarte and Hartman 1974, Nichols and Keeney 1976b) and the roots (Barko and Smart 1980). As a result, the complex interrelationships of mineral uptake, translocation, storage and secretion by submersed hydrophytes and the availability of minerals in their environment are poorly understood. Consequently, attempts to correlate mineral availability in the aquatic environment with the mineral content of submersed hydrophytes have been inconclusive (Adams et al. 1973).

Unfortunately, many researchers investigating mineral dynamics in aquatic plants and the availability of minerals in the aquatic environment have ignored the influence of sampling time on their results (Kimball and Baker 1980). The purpose of this study is to quantify the importance of seasonality on changes in the mineral content of six different plant parts in the submersed hydrophte, Myriophyllum heterophyllum Michx. Our study (1) determines seasonal ranges in mineral content for the six different plant structures, (2) defines the seasonal fluctuations in mineral content, (3) compares the mineral content between the six different plant structures, (4) quantifies the seasonal changes in mineral ratios, and (5) examines some of the reasons for these seasonal changes.

Quantification of the submersed macrophyte's nutrient pool also yields information applicable to their management. The effectiveness of aquatic weed harvesting in removing minerals from the aquatic environment can be estimated from tissue mineral content analysis. Submersed macrophytes are also little grazed. Consequently, the decay of aquatic plants, either by senescence or when induced by chemical herbicide treament, is an important avenue for the accumulated nutrients to enter the littoral zone.

Materials and Methods

Study Site

Lees Mill Cove is a relatively undisturbed, 8 ha embayment of water located at the northwest end of Lake Winnipesaukee (site 35, Figure 1), New Hampshire USA ($A = 179$ km^2, $\bar{z} = 14$ m). The cove's shoreline is rocky, has sparse human development and is dominated by a mixed deciduous - conifer forest (Figure 3). The maximum depth in the cove is 5 m, and thermal stratification is absent. The sediments have a fine, silty consistency. The lakewater is acidic (pH ~ 6.6) and dissolved salt concentrations are low (specific conductance = $22 - 67$ μmho cm^{-1}, 25°C; alkalinity = 7 mg l^{-1} $CaCO_3$; Ca = $3 - 5$ mg l^{-1}). Water transparency is moderate (Secchi disc = $3 - 4$ m), because of natural dissolved organic matter. Plant samples were collected from two locations, sites 1180 and 1185 (Figure 3).

Sampling and Chemical Analysis

Myriophyllum heterophyllum plant samples were collected 14 times from June 1979 through July 1980. Plants were collected by SCUBA during ice-free months, and with a grappling hook through the ice during the winter. The plants were dissected into six sections 5 to 10 cm long: root, stem immediately above the roots, mid-stem, sub-apical stem, apex, and emergent flowering stem (Fig. 4). Three to five root or stem pieces constituted an observation and three replicate observations made up a sample for each plant structure and sample site location. Detritus and epiphytes were removed with a tap water rinse. The samples were dried for 24 hrs at 105°C in a forced-draft oven, weighed and ashed for 7 hrs at 550°C and reweighed.
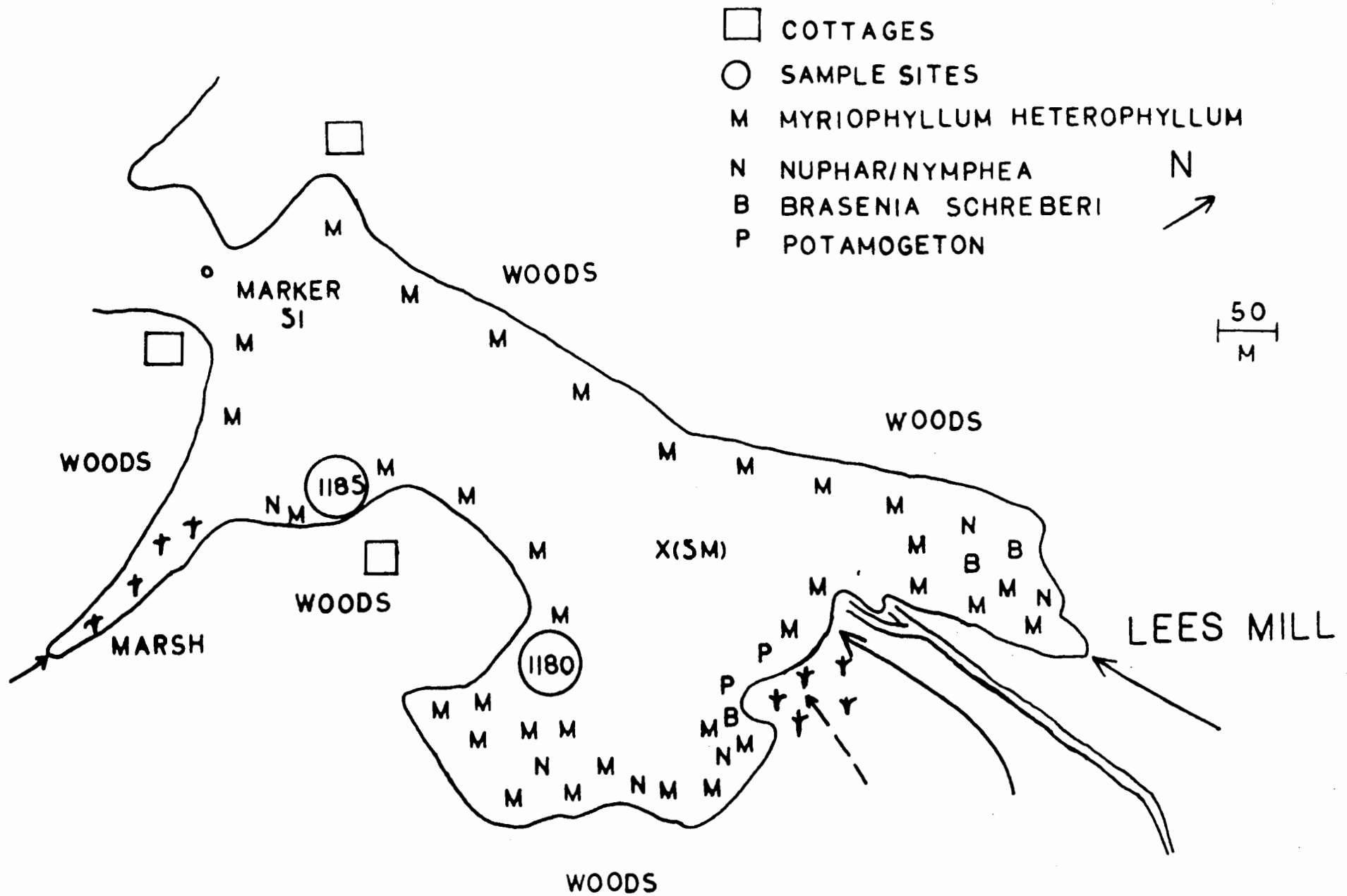
Figure 3. M. heterophyllum sample site locations at Lees Mill in Lake Winnipesaukee, NH.

FLOWER {

APEX {
SUB-APEX {

MID-STEM {

LOWER STEM {

ROOT {

I CM.
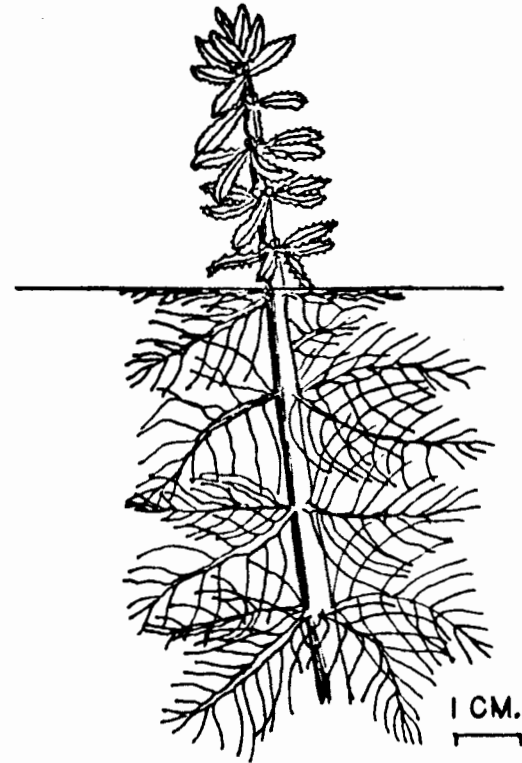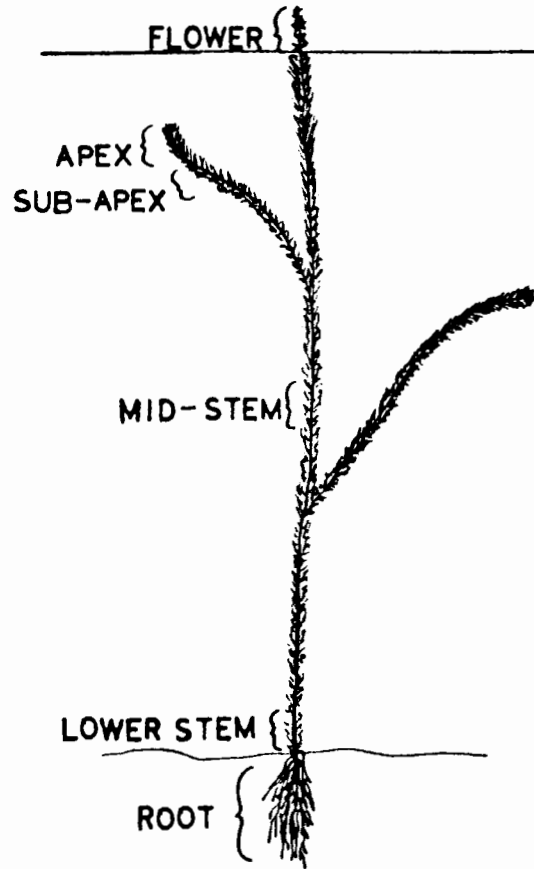
MYRIOPHYLLUM

HETEROPHYLLUM

Figure 4. Structures analyzed for ash and mineral content.

The minerals sodium, calcium, magnesium, iron, manganese, zinc, copper, and lead were extracted by boiling the ash in 50 ml 5% HCl for 20 - 30 min and then analyzed on a Perkin-Elmer Model 306 atomic absorption spectrophotometer calibrated with standard solutions for each metal. Dilutions were made when necessary with double distilled water. A 2% lanthanum solution was aspirated with the calcium samples. Phosphorous was determined from the tissue digest with the colorimetric reaction of ammonium molybdate and potassium antimonyl tartrate-ascorbic acid, modified from Golterman (1969). Absorbance was read at 650 nm on a Fisher electrophotometer with 5 cm cuvets. Ash content was determined gravimetrically. All results are expressed as a percentage dry weight, because calcium carbonate deposition does not occur in the acidic, soft waters of Lake Winnipesaukee.

Statistical Analysis

An ANOVA (STATPK program, University of New Hampshire DEC-10 System) was calculated for each sample date to assess the differences in mineral content between the six plant structures sampled. The interaction between plant structure and sample site was also determined. Because replicate observations for the different plant structures at each sample site were not necessarily from the same plant, they were treated as a random factor nested within site location, in a two-level nested (Model 1) ANOVA (Sokal and Rohlf 1969). An orthogonal comparison test was applied to elements whose plant structure means differed significantly (Steel and Torrie 1960; UNSQSH program, University of New Hampshire DEC-10 System). Orthogonal comparisons on sampling dates without emergent flowering stems were (1) root vs. all other tissues, (2) apex vs. sub-apex, (3) root vs. stem immediately above the root, and (4) apex vs. all other tissue. The additional orthogonal comparison of emergent flowering stem vs. all other tissues, was made when flowering emergent tissue was sampled.

Results

Elemental Composition

Potassium and sodium dominated the actively growing apical region of Myriophyllum heterophyllum, followed by calcium, magnesium and phosphorus. Least abundant were iron, manganese, zinc, copper and then

lead. The lower stem had a similar composition, with the exception that iron and manganese comprised a greater part of the biomass than magnesium. In the roots, iron greatly exceeded all other elements, and lead exceeded copper. Calcium was the dominant element in the emergent floral stem (Table 3). Each element's relative contribution within a specific plant structure changed little seasonally.

The annual % dry weight range for ash and the ten minerals are presented in Table 4. The magnitude of each element's annual range, expressed as a maximum/minimum ratio, was similar in the different submersed structures for ash (two-fold), magnesium (two-fold), zinc (three-fold) and manganese (3-5 fold). Phosphorus, sodium, potassium, calcium and iron content had increasing seasonal variability from the roots to the apex. Trends in seasonal variability for copper and lead were obscure, because of their low concentrations which frequently approached the lower limits of detection. Seasonal variability for the apices was similar to 1976-1978 apical data from M. heterophyllum (Kimball and Baker 1980).

Seasonal Changes in Mineral Content

All submersed structures exhibited a maximum ash content in the early spring and a summer minimum. No temporal changes in floral stem ash content were discernible (Fig. 5). Maximum phosphorus concentrations in the apex occurred in the spring and early autumn. Phosphorus content and its seasonal variation declined basipetally. Phosphorus levels in the emergent stem declined rapidly, following the development of the flowering stem in June (Figure 5). The maximum sodium and potassium values in the submersed stem and apex occurred from late spring to summer. Seasonal variation in the roots was obscure for sodium and characterized by a summer peak for potassium (Figure 6). Calcium and magnesium had maximum summer values in all submersed structures (Figure 7). The calcium content in the emergent floral stem increased during the summer, until the emergent stem senesced. All submersed structures had a late winter to early spring maximum iron and manganese content (Figure 8). The zinc and copper values suggested a spring to early summer maximum in all submersed structures (Figure 9), while lead was frequently below the limits of detection, except in the roots (Figure 10). No temporal trends were observed for iron, manganese, zinc, copper and lead in the emergent floral stem.

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Table 3. Ranked Importance of Ten Minerals in Different
Plant Structures of M. heterophyllum, based on % dry wt.

Structure	Ranking
Emergent Floral Stem	Ca > K > Na > P > Mg > Mn > Fe > Zn > Cu > Pb
Apex	K > Na > Ca > P > Mg > Fe ≥ Mn > Zn > Cu > Pb
Sub-Apex	K ≥ Na > Ca > P > Mg > Fe ≥ Mn > Zn > Cu > Pb
Mid-Stem	K > Na > Ca > Fe ≥ Mn ≥ P ≥ Mg > Zn > Cu = Pb
Lower Stem	K > Na > Ca > Fe > Mn > Mg ≥ P > Zn > Cu ≥ Pb
Root	Fe > K > Na > Ca > P > Mg > Mn > Zn > Pb > Cu
Adventitious Root	K > Na > Ca > Mg > Mn > P > Fe > Zn > Pb > Cu

TABLE 4. SEASONAL TRENDS AND RANGES IN MINERAL % DRY WEIGHT CONTENT FOR DIFFERENT STRUCTURES OF

MYRIOPHYLLUM HETEROPHYLLUM DURING 1979 – 1980 (Minimum – Maximum % dry weight, Max./Min. ratio)

	Flowering Stem	Submersed Apex	Sub-Apex	Mid-Stem	Stem just above Root	Root
Ash	Not discernible	Spring peak, summer minimum	Spring peak, summer minimum	Spring peak, summer minimum	Spring peak, summer minimum	Spring peak, summer minimum
	(10.73–13.60, 1.3)	(10.43–18.83, 1.8)	(12.46–21.94, 1.8)	(16.37–28.21, 1.7)	(15.28–26.78, 1.8)	(16.34–28.71, 1.8)
P	Summer decline	Spring and fall peak	Spring peak	Suggests spring-summer increase	Suggests spring-summer increase	Suggests spring-summer increase
	(0.18–0.44, 2.5)	(0.25–0.58, 2.3)	(0.21–0.41, 2.0)	(0.18–0.28, 1.6)	(0.13–0.23, 1.7)	(0.15–0.28, 1.9)
Na	Summer decline	Late spring – early summer peak	Late spring – early summer peak	Summer peak	Summer peak	Not discernible
	(0.32–1.08, 3.4)	(0.78–2.27, 2.9)	(0.89–2.70, 3.0)	(1.22–2.31, 1.9)	(1.05–1.74, 1.7)	(0.46–0.92, 2.0)
K	Suggests summer decline	Late spring – early summer peak	Late spring – early summer peak	Suggests late spring – early summer peak	Summer peak	Summer peak
	(0.72–1.44, 2.0)	(1.35–3.11, 2.3)	(1.38–3.06, 2.2)	(2.0–3.28, 1.6)	(1.88–3.12, 1.7)	(1.46–2.30, 1.6)
Ca	Summer increase	Summer peak	Summer peak	Summer peak	Summer peak	Suggests summer peak
	(2.36–4.10, 1.7)	(0.67–1.57, 2.3)	(0.77–1.56, 2.0)	(0.86–1.89, 2.2)	(0.97–1.59, 1.6)	(0.49–0.72, 1.5)
Mg	Late summer decline	Summer peak	Summer peak	Summer peak	Spring peak	Spring peak
	(0.19–0.39, 2.1)	(0.16–0.31, 1.9)	(0.16–0.34, 2.2)	(0.16–0.25, 1.5)	(0.12–0.25, 2.2)	(0.10–0.17, 1.7)
Fe	Not discernible	Late winter – spring peak	Late winter – spring peak	Late winter – spring peak	Suggests late winter spring peak	Late winter – spring peak
	(0.03–0.08, 2.5)	(0.04–0.27, 6.3)	(0.09–0.36, 4.2)	(0.13–0.42, 3.3)	(0.08–1.47[a], 17.3)	(2.83–7.95, 2.8)
Mn	Not discernible	Late winter – spring peak	Late winter – spring peak	Late winter – spring peak	Late winter – spring peak	Late winter – spring peak
	(0.038–0.111, 2.9)	(0.042–0.212, 5.1)	(0.088–0.362, 4.1)	(0.114–0.530, 4.6)	(0.185–0.519, 2.8)	(0.057–0.279, 4.9)
Zn	Not discernible	Spring – early summer peak	Spring – early summer peak	Spring – early summer peak	Spring – early summer peak	Spring – early summer peak
	(0.008–0.026, 3.4)	(0.009–0.032, 3.8)	(0.009–0.038, 4.1)	(0.015–0.044, 2.9)	(0.015–0.060, 4.1)	(0.015–0.048, 3.3)
Cu[b]	Not discernible	Suggests spring peak	Suggests spring peak	Suggests spring peak	Suggests spring peak	Suggests spring peak
	(0.0001 – 0.0010)	(0.0001 – 0.0020)	(0.0001 – 0.0020)	(0.0002 – 0.0014)	(0.0001 – 0.0016)	(0.0003 – 0.0024)
Pb[b]	Not discernible	Not discernible	Not discernible	Not discernible	Not discernible	Suggests summer peak
	(nd – 0.0011)	(nd – 0.0027)	(nd – 0.0028)	(nd – 0.0033)	(nd – 0.0037)	(0.0040–0.0115, 2.9)

[a] Sample possibly contaminated   [b] Values at lower limits of detection   nd = not detectable

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MYRIOPHYLLUM
HETEROPHYLLUM

ASH

FLOWER
APEX
SUB-APEX
MID-STEM
LOWER STEM
ROOT

% DRY WEIGHT
0 10 20 30 40

VI | VII | VIII | IX | X | XI | XII | I | II | III | IV | V | VI | VII

1979   1980
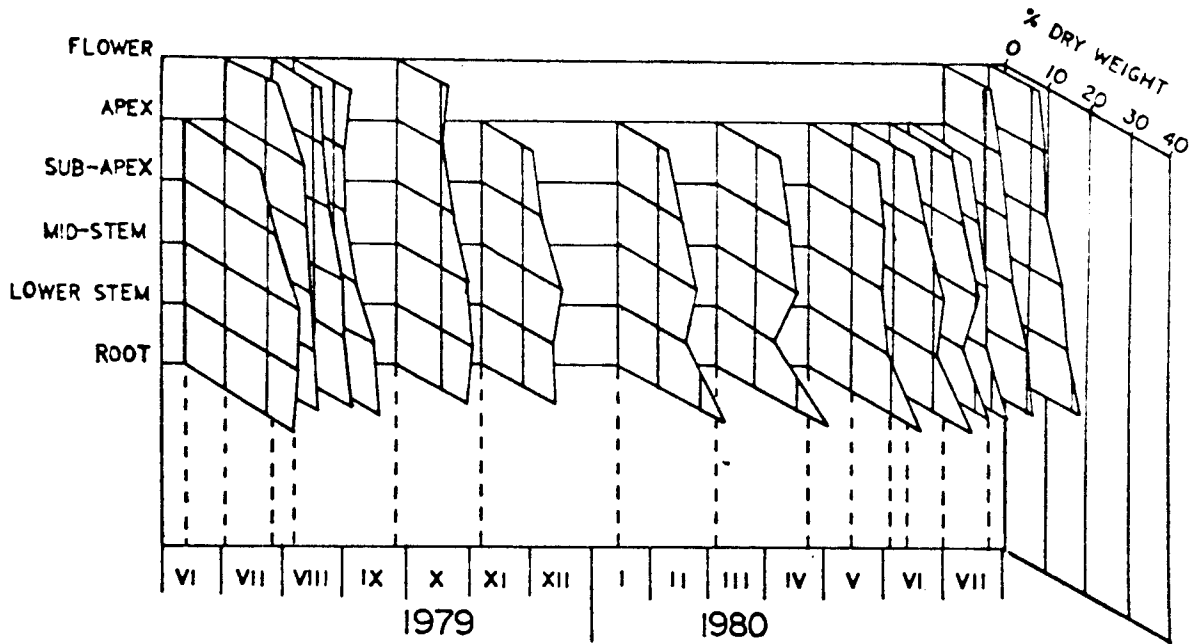
MYRIOPHYLLUM
HETEROPHYLLUM

PHOSPHORUS

FLOWER
APEX
SUB-APEX
MID-STEM
LOWER STEM
ROOT

% DRY WEIGHT
0 .2 .4 .6 .8

VI | VII | VIII | IX | X | XI | XII | I | II | III | IV | V | VI | VII

1979   1980
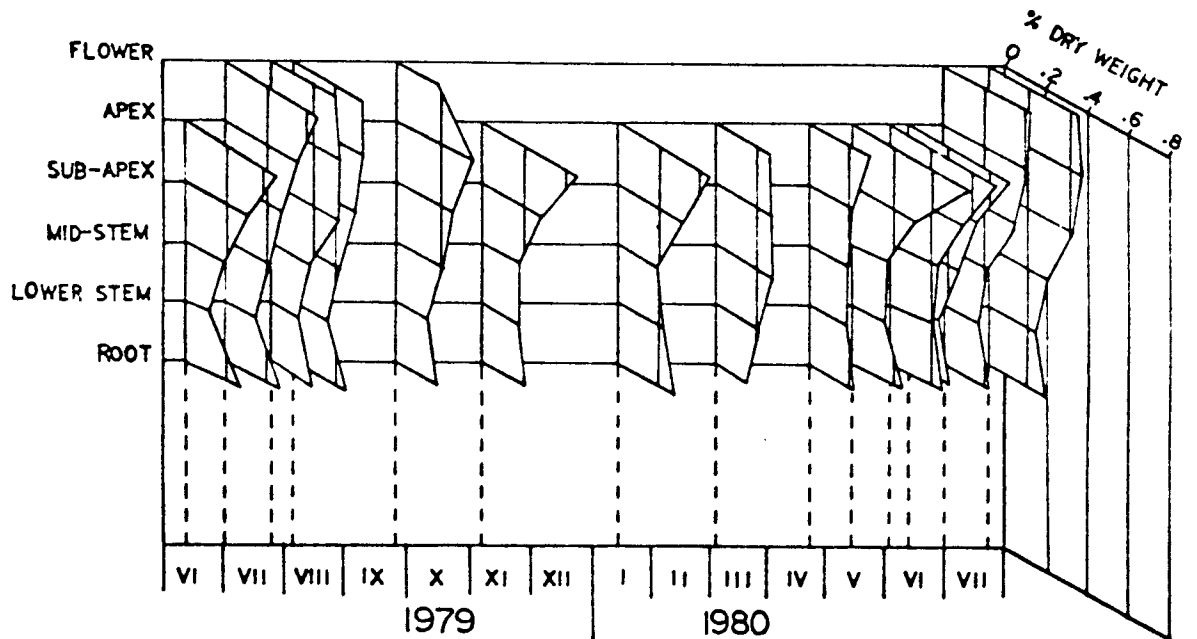
Figure 5 .. Ash and P % dry wt content in M. heterophyllum

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MYRIOPHYLLUM HETEROPHYLLUM   SODIUM

MYRIOPHYLLUM HETEROPHYLLUM   POTASSIUM
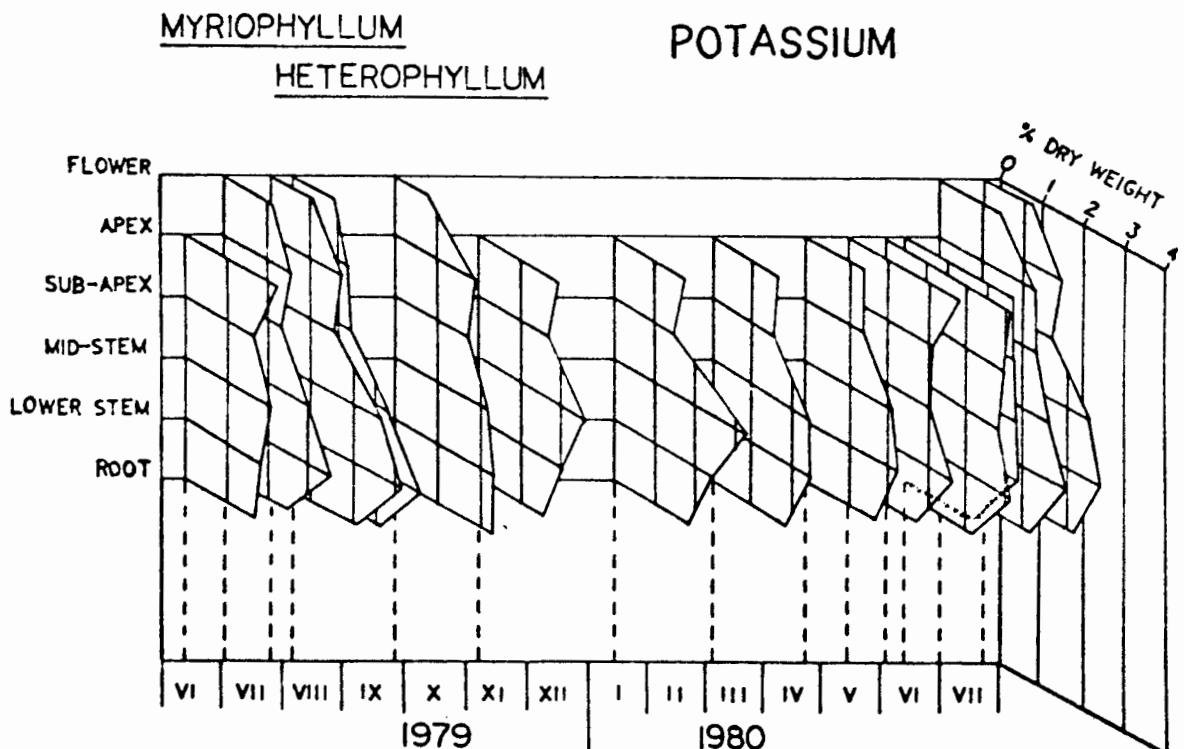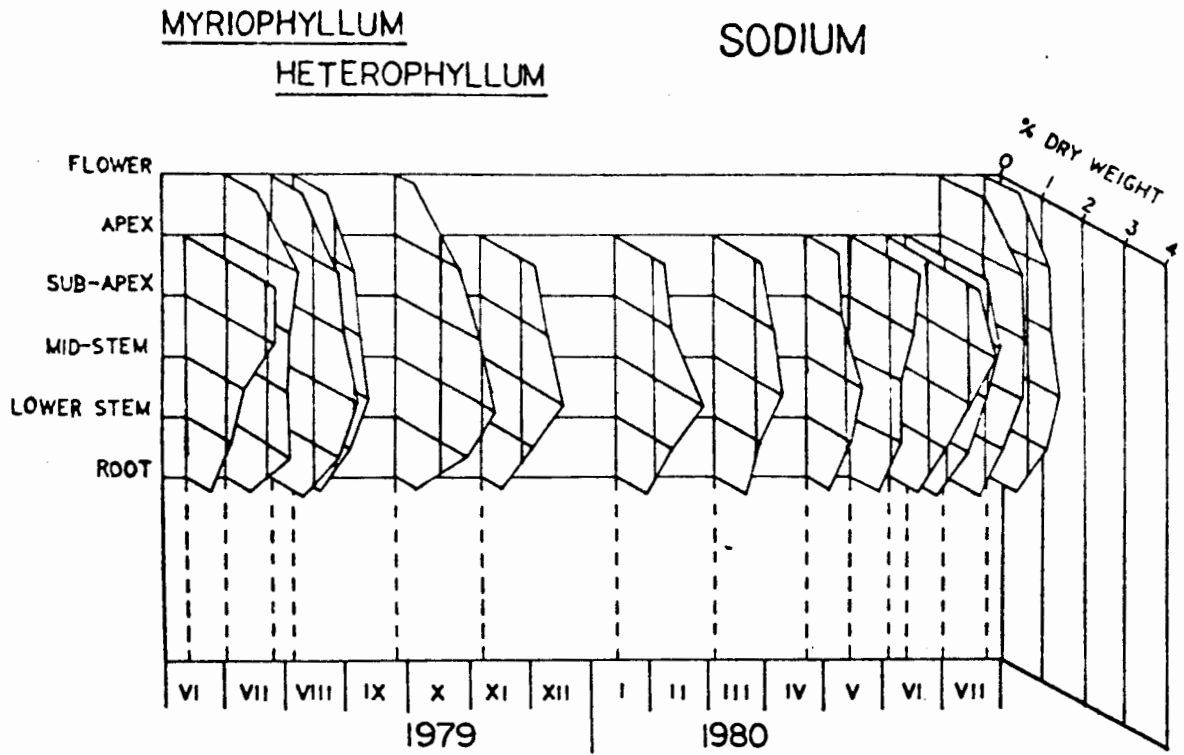
Figure 6. Na and K % dry wt content in M. heterophyllum
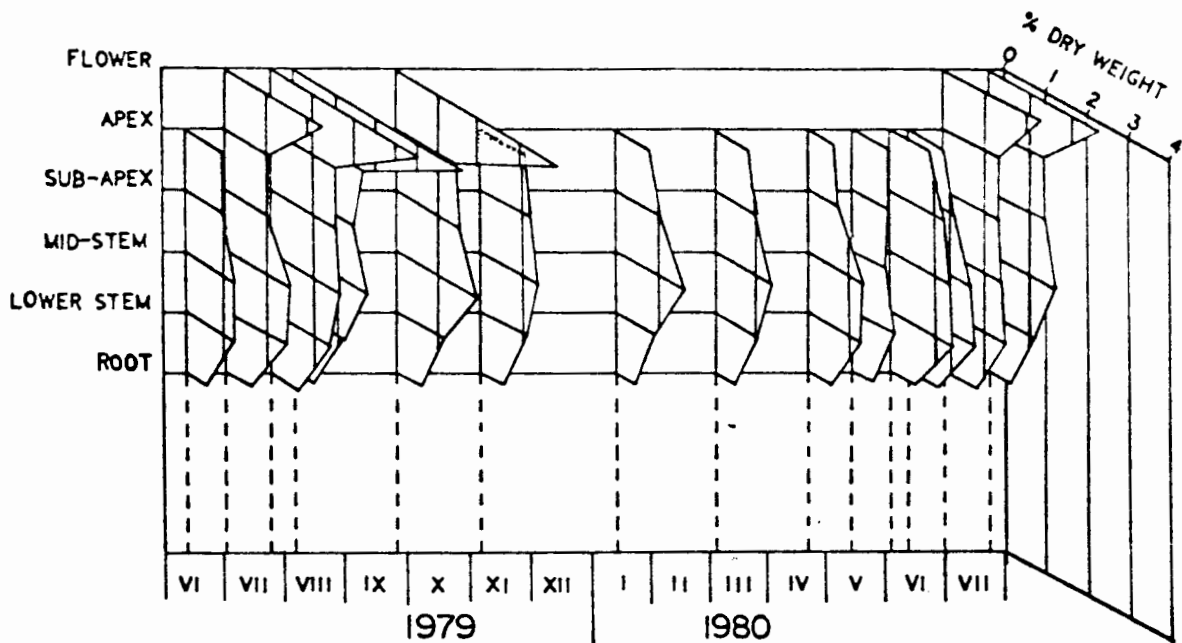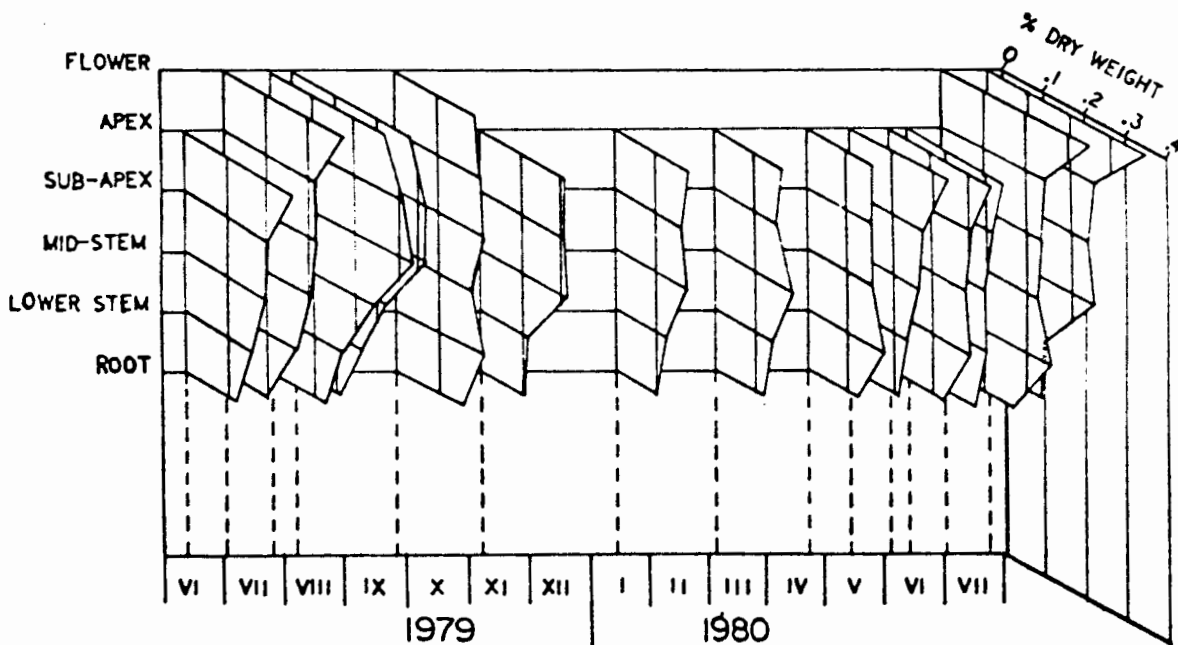
Figure 7 . Ca and Mg % dry wt content in M. heterophyllum

MYRIOPHYLLUM
HETEROPHYLLUM

IRON

MYRIOPHYLLUM
HETEROPHYLLUM

MANGANESE
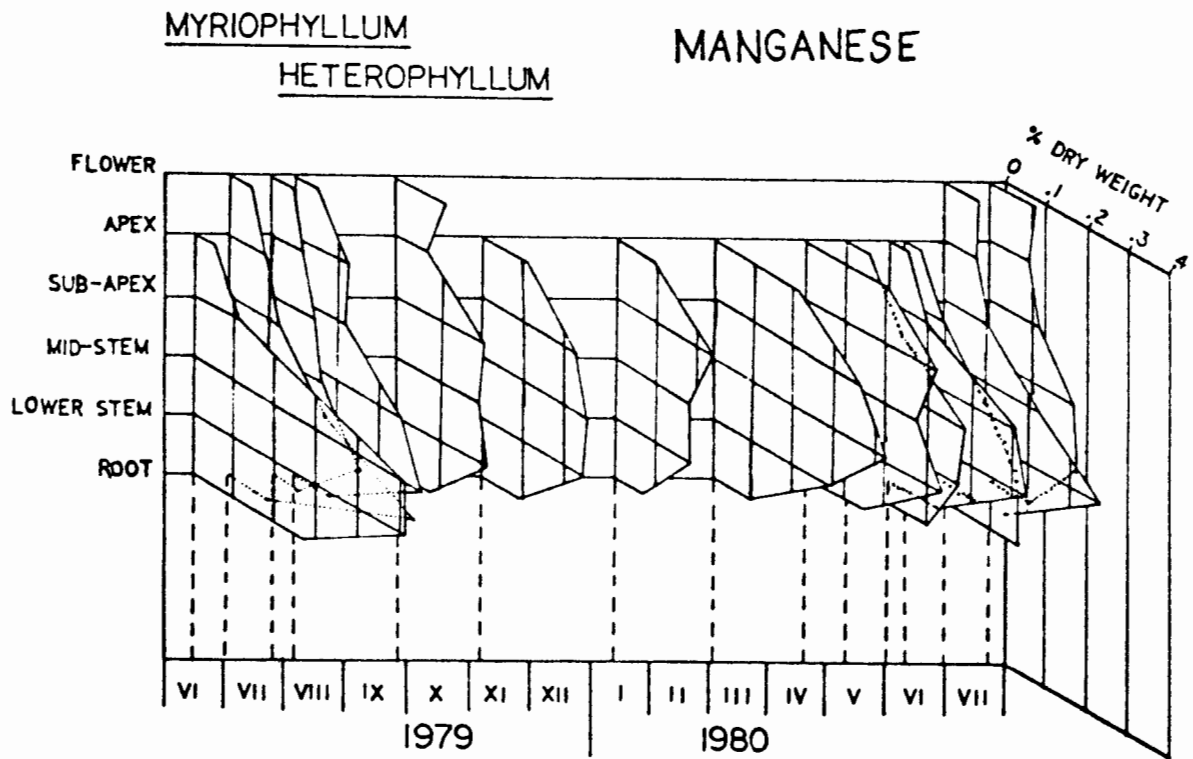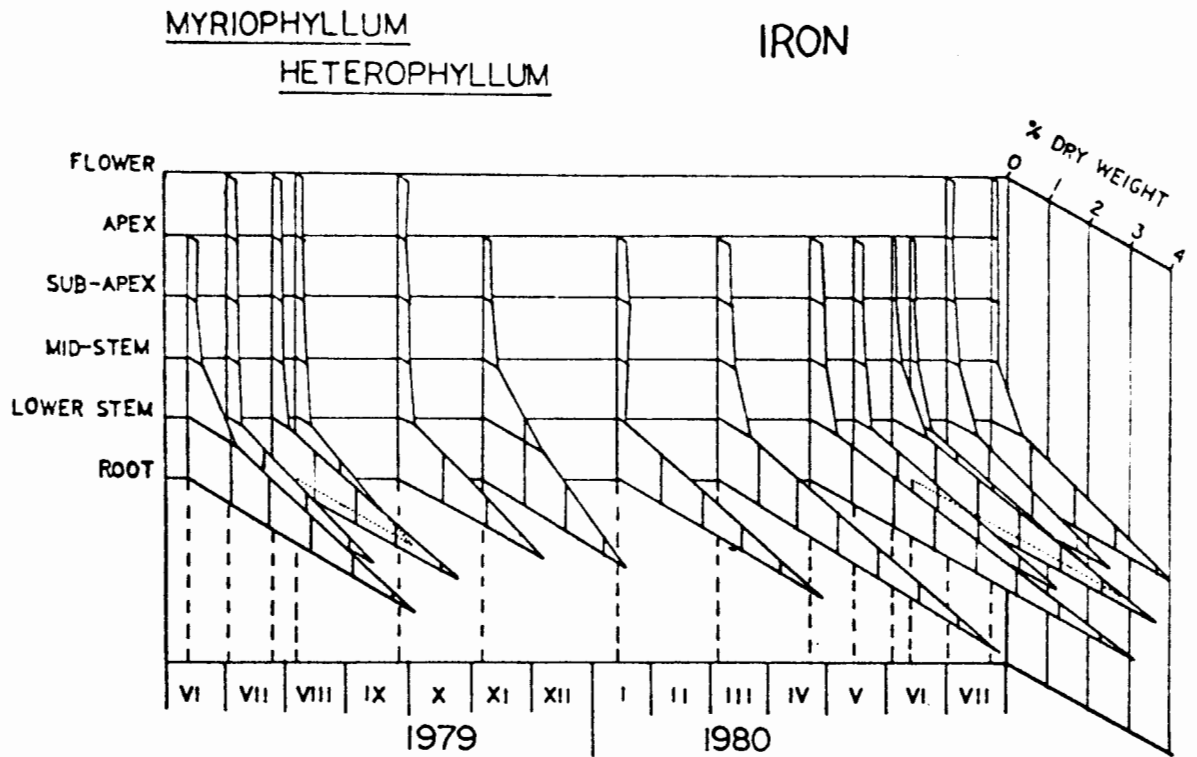
Figure 8 . Fe and Mn % dry wt content in M. heterophyllum

MYRIOPHYLLUM HETEROPHYLLUM   ZINC

MYRIOPHYLLUM HETEROPHYLLUM   COPPER

Figure 9 .   Zn and Cu % dry wt content in M. heterophyllum
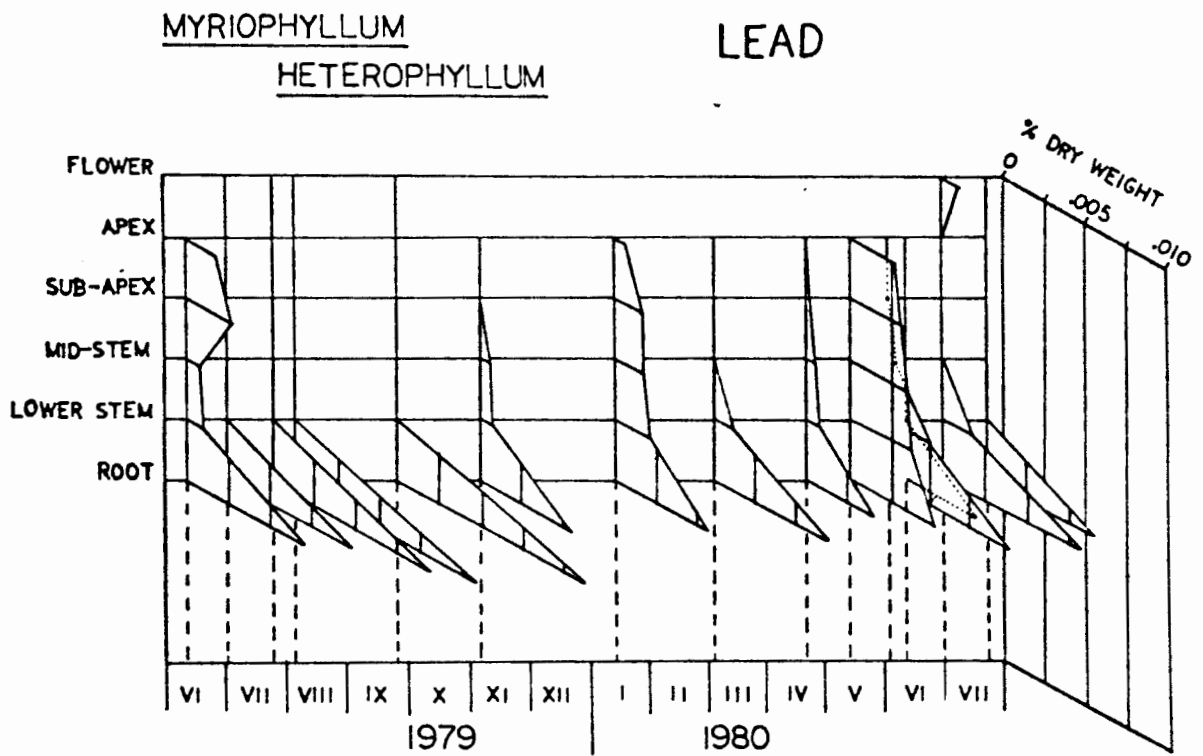
Figure 10. Pb % dry wt content in M. heterophyllum

Mineral Content Differences Between Plant Structures

During most seasons, ash, phosphorus and all metals except copper differed significantly between the plant structures analyzed (Appendix 1). Differences between the two sample sites in plant tissue mineral content were generally insignificant (Appendix 2). Ash concentrations in the emergent stem were significantly lower than in the stem and root. Root and lower stem ash values were similar during the growing season, but the ash content in the roots was significantly greater during autumn through spring. Phosphorus values were significantly higher in the submersed apices and the emergent floral stems, while minimal values consistently occurred in the lower stem and root. Sodium had significantly lower concentrations in the root and emergent floral stem, while the highest sodium concentrations generally occurred in the main stem. Similarly, potassium had significantly lower values in the roots than in the lower stem, and higher values generally in the stem portion.

A dominant feature of calcium was its significantly higher concentration in the emergent floral stem, and very low values in the roots. Older mid-stem parts of the plant generally had slightly elevated calcium concentrations compared to the apical region. Though not as pronounced as calcium, root values for magnesium were also lower, particularly when compared to other plant structures. Iron was characterized by its dramatically higher values in the roots. Apical and root levels of manganese were generally lower than in the stem. During the winter, zinc levels were similar throughout the plant, while higher levels in the stem were more frequent during the growing season. Lead, like iron, also had greatly increased concentrations in the roots. Plant structure differences in copper content were obscure. Mean separations by orthogonal comparisons between the different plant structures are listed in Appendix 3.

Mineral Ratio Variability

Variations in mineral ratios, using % dry weight, occurred both temporally and between plant structures in _Myriophyllum heterophyllum_. Throughout the sampling year, there was an increase in the K/Na ratio from the sub-apex to the roots. The K/Na ratio was higher in the emergent floral stems, than in the submersed apices (Table 5).

Calcium was the dominant divalent cation in the emergent floral stem and it contributed to a greater part of the chemical composition than magnesium as the summer progressed. Prior to floral development in May-June, the Ca/Mg ratios in the submersed apices were at their lowest. The lower part of the stem, which is stiffer structurally, also had a higher Ca/Mg ratio (Table 6).

A declining K/Ca ratio has been used to determine the age of plant parts in emergent aquatic macrophytes, with the highest K/Ca values occurring during the growth phase (Dykyjova 1978). A similar trend occurred in M. heterophyllum, with the maximum K/Ca values in the upper stem and apex during May and June. As the emergent floral stem senesced in late summer, there was a corresponding decline in the K/Ca ratio (Table 7). The Fe/Mn ratio was lowest in the emergent floral stem and highest in the lower stem, particularly in the roots (Table 8). The % dry weight ratios can be converted to atomic ratios by multiplying with the following coefficients: K/Na x 1.70, Ca/Mg x 1.65, Fe/Mn x 1.02 and K/Ca x 0.98.

Discussion

Intraspecific Mineral Content Comparisons

A large number of papers on the chemical analysis of aquatic macrophytes has been reviewed by Hutchinson (1975). The studies reveal considerable variation in inorganic composition in the same species from different environments and the intraspecific differences have been attributed to mineral availability in the environment. The data in this study suggest that the type of plant structure and season can cause much of the variability reported in the literature. For example, Riemer and Toth (1969) report iron to be the dominant metal in M. heterophyllum, while Boyd (1970) reports sodium. The former study included whole plant material, while the latter sampled only the green apical portion in September. The high iron content (2.4% dry wt) in Riemer and Toth's study results from the inclusion of lower stem material which can be an order of magnitude higher in iron content than the upper stem (Figure 8). Furthermore, the sodium content will change seasonally more than twofold (Table 4). By comparing Boyd's South Carolina and our New Hampshire mineral content data, using similar sample dates and plant structures, many of the differences in mineral content become obscure. Therefore, mean-

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TABLE 5. SEASONAL CHANGES IN THE K/NA RATIO IN DIFFERENT STRUCTURES OF MYRIOPHYLLUM HETEROPHYLLUM

Date	Flowering stem	Apex	Sub-apex	Mid-stem	Lower stem	Root	Adventitious root
13-VI-79	- -	1.0	0.8	1.5	1.6	2.9	- -
2-VII-79	1.5	0.9	0.8	1.2	1.6	2.7	- -
25-VII-79	1.4	1.1	0.9	1.3	1.9	2.6	- -
6-VIII-79	1.3	0.9	0.9	1.3	2.2	3.3	- -
26-IX-79	2.2	1.1	0.9	0.9	1.4	5.0	- -
6-IX-79	- -	1.5	1.1	1.4	1.7	2.9	- -
13-I-80	- -	1.5	1.2	1.6	1.8	2.4	- -
3-III-80	- -	1.4	1.1	1.4	2.1	2.6	- -
22-IV-80	- -	1.8	1.6	1.7	2.1	3.3	- -
12-V-80	- -	1.5	1.4	1.6	2.1	2.6	- -
3-VI-80	- -	1.4	1.1	1.4	2.1	3.0	- -
10-VI-80	- -	1.3	1.2	1.4	1.8	2.4	- -
30-VI-80	1.3	1.2	1.2	1.4	2.0	2.4	- -
21-VII-80	1.4	1.2	1.1	1.5	2.0	3.0	2.1

TABLE 6. SEASONAL CHANGES IN THE CA/MG RATIO IN DIFFERENT STRUCTURES OF <u>MYRIOPHYLLUM</u> <u>HETEROPHYLLUM</u>

Date	Flowering stem	Apex	Sub–apex	Mid–stem	Lower stem	Root	Adventitious root
13-VI-79	– –	3.5	4.2	6.0	7.7	4.6	– –
2-VII-79	8.3	4.9	4.7	7.8	7.8	6.4	– –
25-VII-79	13.0	5.1	4.6	7.2	8.7	5.6	– –
6-VIII-79	14.1	4.8	4.6	7.7	8.2	5.7	– –
26-IX-79	21.4	7.1	7.3	10.1	5.6	3.9	– –
6-IX-79	– –	5.0	6.2	6.1	8.8	5.4	– –
13-I-80	– –	5.0	7.3	9.8	7.9	4.7	– –
3-III-80	– –	5.1	6.5	7.4	7.6	4.5	– –
22-IV-80	– –	4.2	4.9	4.2	7.2	4.4	– –
12-V-80	– –	3.9	5.0	5.1	7.0	4.3	– –
3-VI-80	– –	3.7	6.6	7.8	7.6	3.9	– –
10-VI-80	– –	3.7	5.2	7.9	8.1	4.3	– –
30-VI-80	6.4	5.3	5.5	6.2	5.6	4.3	– –
21-VII-80	7.1	5.1	5.6	6.3	8.0	4.4	2.3

TABLE 7. SEASONAL CHANGES IN THE K/CA RATIO IN DIFFERENT STRUCTURES OF <u>MYRIOPHYLLUM HETEROPHYLLUM</u>

Date	Flowering stem	Apex	Sub - apex	Mid - stem	Lower stem	Root	Adventitious root
13-VI-79	- -	2.2	1.8	1.7	1.5	3.0	- -
2-VII-79	0.5	1.4	1.3	1.3	1.8	2.3	- -
25-VII-79	0.3	1.1	1.0	1.5	2.0	2.9	- -
6-VIII-79	0.2	0.9	1.0	1.3	2.4	3.3	- -
26-IX-79	0.2	1.3	1.1	1.1	2.2	3.7	- -
6-IX-79	- -	1.9	1.4	1.9	2.1	2.6	- -
13-I-80	- -	1.9	1.3	1.9	2.5	3.7	- -
3-III-80	- -	1.9	1.5	1.7	2.2	3.3	- -
22-IV-80	- -	2.0	1.8	1.6	1.7	3.3	- -
12-V-80	- -	2.9	2.3	2.3	2.6	3.3	- -
3-VI-80	- -	3.2	2.3	2.0	2.0	3.7	- -
10-VI-80	- -	3.0	2.4	1.8	1.7	2.4	- -
30-VI-80	0.6	1.8	1.8	1.9	2.1	3.1	- -
21-VII-80	0.4	1.4	1.2	1.6	2.5	3.9	2.7

TABLE 8. SEASONAL CHANGES IN THE FE/MN RATIO IN DIFFERENT STRUCTURES OF <u>MYRIOPHYLLUM HETEROPHYLLUM</u>

Date	Flowering stem	Apex	Sub-apex	Mid-stem	Lower stem	Root	Adventitious root
13-VI-79	- -	2.9	2.1	0.7	2.3	21.1	- -
2-VII-79	0.6	2.3	2.0	0.9	0.7	40.6	- -
25-VII-79	0.9	1.2	1.4	1.1	1.3	75.6	- -
6-VIII-79	0.6	1.3	1.6	0.6	0.8	34.1	- -
26-IX-79	0.4	0.7	0.6	0.9	1.4	42.4	- -
6-IX-79	- -	1.0	0.8	1.0	5.9	37.8	- -
13-I-80	- -	1.2	1.1	1.1	0.5	72.3	- -
3-III-80	- -	1.0	0.9	1.0	2.8	74.8	- -
22-IV-80	- -	1.3	1.2	1.1	2.0	57.8	- -
12-V-80	- -	1.0	1.0	1.1	2.4	24.2	- -
3-VI-80	- -	1.0	0.9	0.7	2.4	52.2	- -
10-VI-80	- -	1.3	1.0	0.9	1.7	18.3	- -
30-VI-80	0.9	1.4	1.6	1.2	1.8	25.3	- -
21-VII-80	0.4	0.9	0.8	0.7	3.6	40.3	0.5

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ingful inter- or intra-specific comparisons of aquatic macrophyte mineral content should only be made using similar sampling seasons and plant structures.

Mineral Storage

There are several mechanisms by which perennial submersed hydro-phytes meet their mineral requirements for growth, including: (a) lux-ury consumption by foliar uptake and storage in the stems, when exces-sive levels of mineral exist in the water column (Gerloff and Krombholz 1966), (b) the development of storage organs, such as Nuphar luteum's rhizomes, which assimilate phosphorus year round and rapidly translocate it acropetally during the growing season (Twilley, Brinson and Davis 1977), (c) the ability to overwinter large proportions of the summer leaf and stem biomass, as a method of conserving minerals in nutrient poor environments without the development of specialized storage organs, as reported for Utricularia purpurea (Moeller 1980) and Lobelia dortmanna (Moeller 1978), and (d) the ability to rapidly take up minerals from nutrient rich sediments or the water column during the growing season.

Though luxury consumption by foliar uptake has been demonstrated for M. heterophyllum (Chagnon and Baker 1979), it is apparently a temporary phemonenon. In situ phosphorus additions to M. heterophyllum colonies during the summer resulted in increased apical concentrations. Following the cessation of nutrient enrichment in late summer, treated and control apices did not differ significantly (Chagnon and Baker 1979, Kimball unpublished). Furthermore, using compartmentalized containers and by adding labeled isotopes, it has been shown that root uptake with acropetal translocation commonly occurs in water milfoil (Bristow and Whitcombe 1971, DeMarte and Hartman 1974, Nichols and Keeney 1976b, and Waisel and Shapira 1971). In these laboratory studies, the roots and shoots were usually presented with equal concentrations of the isotope, which favors foliar uptake, an unusual condition in nature.

There was little evidence in this study of winter storage of miner-als in roots or stems of M. heterophyllum, except possibly iron and man-ganese. However, the increased iron and manganese concentrations during late winter through spring probably represent chemical precipitation on the outer surface of the plant and not mineral storage. The importance of water milfoil's root system as a storage organ is also doubted, be-cause the roots represent only 10% of the plant's total biomass (Barko

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and Smart 1980). Nichols and Keeney (1976a) disagree with this conclusion, and suggest that nitrogen is accumulated during the winter by M. spicatum. Unfortunately, like many mineral studies with aquatic plants, they took no samples from mid-autumn through spring and they derive their conclusions from the measured maximum nitrogen levels during autumn and spring. Consequently, their conclusions regarding maintenance of high tissue nitrogen levels throughout the winter are inconclusive. In this study, phosphorus tissue levels were maximal in the spring and autumn, but were not maintained throughout the winter (Figure 5).

Myriophyllum heterophyllum frequently overwinters considerable green biomass. Unlike U. purpurea and L. dortmanna, many of M. heterophyllum's stems break free during the spring. Because fragmentation is an important means of vegetative reproduction in water milfoil (Aiken, Newroth and Wile 1979), it is difficult to determine whether the overwintered stems function as a mechanism to preserve minerals for spring growth or to colonize new areas early in the year.

In situ experiments demonstrate an overwhelming preference for uptake of phosphorous from the sediments by M. spicatum (Carignan and Kalff 1980). Barko and Smart (1980) showed that water milfoil's roots can rapidly mobilize phosphorus directly from the sediments to the stem and leaves to meet growth requirements. Such results concur with the present study. The phosphorus levels in the apices and upper stems rapidly increased during early spring, while those of the roots changed little through the year and was significantly lower than in the apices. In addition, the sediments harboring water milfoil in Lake Winnipesaukee have considerable concentrations of phosphorus (Chagnon and Baker 1979).

The results suggest that M. heterophyllum and M. spicatum can meet their mineral requirements by rapidly taking up minerals from nutrient rich sediments during or immediately prior to the growing season. Thus, mineral storage is not of primary importance, and water milfoil has the capacity to rapidly colonize nutrient rich sediments in the littoral zone and become a major nuisance. Therefore, the growth of water milfoil should be sensitive to chemical inactivation of the nutrients during the spring and early summer as a means of weed control, particularly if the old stem biomass were harvested the previous autumn.

Emergent Stem Chemistry

The calcium content in the emergent floral stems was significantly higher than in submersed parts, and increased with the age of the tissue (Figure 7). It is generally recognized that calcium is not easily redistributed from older tissues toward younger plant parts, because of its low mobility in the phloem (Clarkson 1974) and its possible metabolic role in countering the production of assimilates and organic acids in mature leaves (Armstrong and Kirby 1979). Calcium provides mechanical strength to tissues, as calcium pectate in the middle lamella (Epstein 1972), though this has been criticized (Gauch 1972). Both the accumulation of calcium in older tissue and its structural role in keeping the emergent floral stem upright in an aerial environment apparently occur in M. heterophyllum.

Magnesium is a relatively transient and mobile cation in plants compared to calcium (Clarkson 1974), a characteristic observed in this study. The Ca/Mg ratio increased with age in the emergent floral stem and from the ontogenetically young submersed apices to the lower stem (Table 6).

Submersed Stem Chemistry

The most abundant cations in the submersed stems of M. heterophyllum were sodium and potassium (Table 3). Compared to the values in the submersed stem, the concentrations of sodium were significantly lower in the emergent floral stem and roots, and potassium values were lower in the roots as compared to the stem (Appendix 3). The high concentration of sodium (1 - 2% dry wt) is characteristic of other submersed hydrophytes, compared to floating hydrophytes and emergent aquatic plants (Boyd 1970, Boyd and Hess 1970, Hutchinson 1975, and Moeller 1978, 1980). Terrestrial higher plants have a marked discrimination against sodium absorption (Clarkson 1974), and their average sodium content is 0.12% dry weight (Hutchinson 1975). The sodium content in halophytes, however, exceeds that of submersed hydrophytes and sodium is preferentially stored in the stem as compared to the roots (Flowers 1975). Terrestrial leaves have a declining K/Na ratio with the aging of the leaves, because of the greater export of potassium than sodium from older to younger leaves (Pitman 1975). In contrast, M. heterophyllum's older tissues frequently had higher K/Na ratios (Table 5).

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Possibly sodium and potassium have a dynamic role in the
movement of water and anions from the roots to the stem. There is much
evidence that submersed hydrophytes move anions and water acropetally
(reviewed by Hutchinson 1975, Sculthorpe 1967, Wetzel 1975), and a Cas-
parian strip is present in the roots (Sculthorpe 1967). It is doubtful
that root pressure or evaporation from leaf surfaces, mechanisms which
drive transpirational flow in terrestrial plants, are functional in sub-
mersed hydrophytes. The xylem is vestigial in the stems, stomata are
absent and evaporation can not occur under water (Sculthorpe 1967). We
speculate that the relatively high sodium and potassium levels in the sub-
mersed stem, compared to the root, functions to develop a negative osmotic
potential sufficient to move water and solutes acropetally in the vascular
bundle from the roots. Shepherd and Bowling (1973) present evidence that
aquatic plants actively accumulate sodium through the roots, which con-
trasts with most terrestrial plants that possess a sodium efflux pump.
In addition, the vascular strand in $\underline{M}$. heterophyllum is coalesced axially
and protected from the hypotonic water medium by the surrounding highly
developed air spaces. For this hypothesis to be correct, it would be
essential for sodium and potassium levels in the stem to peak during the
growing season when solute demands are greatest and this was observed
(Figure 6). A system of negative osmotic potential developed by a high
concentration of salts in the stem operates in halophytes (Flowers 1975).

Root Chemistry

It is paradoxical that dense beds of $\underline{M}$. heterophyllum thrive in the
oligotrophic waters of Lake Winnipesaukee. However, anaerobic conditions
in the sediments greatly increase the solubility and availability of
phosphate and ferrous ions in interstitial waters (Wetzel 1975). During
the summer, sapropel dispersed in the gyttja of the sediments was observed
at the study site, indicative of a reducing environment. Submersed hydro-
phyte roots can survive in the anaerobic environment of the sediments and
utilize the sediment nutrient pool, by diffusing photosynthetically pro-
duced oxygen from the stem to the root apex in the lacunae (Grace and
Wetzel 1978).

Armstrong (1967) reports that actively growing roots in waterlogged
bog plants oxidize ferrous iron and cause its precipitation as ferric
iron by diffusion of oxygen or the secretion of oxidizing enzymes. The
oxidizing reactions may also remove other potentially harmful phytotoxins

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in hydrosoils, such as reduced manganese, sulfide and possibly organic products. The immobilization occurs within the roots, but deposition apparently takes place on the root surface and in the rhizosphere. Rapid reduction in oxygen permeability and enzyme secretion of the root wall occurs in the root's subapical region in wetland species (Armstrong 1978). Consequently, precipitated ferric iron may diminish around older, inactive roots, because it is resolubilized by the sediments' reducing environment (Armstrong 1967). Such reactions explain the high iron content in M. heterophyllum roots. The anomaly is that, by creating an aerobic rhizosphere such that the ferrous iron is oxidized, the solubility and hence availability of phosphate in the adjacent interstitial waters would theoretically be diminished.

Unlike iron, manganese is soluble and less likely to be oxidized when the pH is below 6 (Stumm and Morgan 1970). No evidence of manganese precipitation or storage in water milfoil roots was observed. Rather the data suggests that manganese is translocated into the stem (Figure 8), possibly to maintain its concentration in the roots below toxic levels.

Lead is usually precipitated to the sediments (Stumm and Morgan 1970). The high lead content in M. heterophyllum roots was possibly concentrated, according to Donnan equilibria, as observed in Potamogeton pectinatus leaves (Sharpe and Denny 1976). Similarly, Elodea canadensis is known to accumulate lead from sediments (Mayes, McIntosh and Anderson 1977). There was no evidence that M. heterophyllum translocated lead acropetally as in P. pectinatus and P. crispus (Welsh and Denny 1979). Copper and zinc were not concentrated in the roots of M. heterophyllum (Figure 9). Welsh and Denny (1979) report extensive acropetal translocation of copper from the roots to the stem, apices and young leaves.

Several studies (Moeller 1978, Ophel and Fraser 1970, Riemer and Toth 1969) have attributed the increased concentration of minerals in the roots to incomplete removal of attached sediment particles during washing. The results of this study indicated that these high levels instead may represent biological precipitation of minerals as a sheath on the roots.

Nutrient Removal by Aquatic Weed Harvesting

Aquatic weed harvesting has the potential to remove growth stimulating nutrients from the sediments. Commercial aquatic weed harvesters effectively harvest to depths of 1 to 1.5 m (Aquamarine Corporation, Wauskesha, Wiscon-

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sin; pers. comm.). We estimate that one summer harvest of $\underline{M}$. $\underline{heterophyllum}$ in Moultonboro Bay, Lake Winnipesaukee would remove 0.39 to 0.59 g P m^{-2} (Appendix 4a). The annual loading rate of phosphorus into Moultonboro Bay is estimated at 0.3 g P m^{-2} yr^{-1} (Resource Planning Associates 1977) and phosphorus levels in the sediments approximate 5.4 to 15.5 g P m^{-2} (Appendix 4b). Therefore, two harvests per year of $\underline{M}$. $\underline{heterophyllum}$ would theoretically take 8 to 23 years to completely deplete the phosphorus pool in the sediments (Appendix 4). We conclude, based on our calculations and other studies (Burton et al. 1979, State of Vermont 1979) that only a long-term, annual harvesting program would reduce phosphorus levels in the sediments sufficiently to limit water milfoil growth.

Summary

Data on the annual variations in ash, phosphorus, sodium, potassium, calcium, magnesium, iron, manganese, copper, zinc and lead content for the submersed hydrophyte, $\underline{M}$. $\underline{heterophyllum}$, are presented. Plant structures sampled were the emergent floral stem, apex, sub-apex, mid-stem, lower stem and roots. Many of the plant structures differed significantly in each mineral sampled. Though the different structures varied in mineral content, the seasonal pulses in mineral content were usually in synchrony between the different structures sampled. The data also suggest that the minerals' seasonal peaks occur annually.

Excluding the emergent floral stem and the roots, sodium and potassium were the dominant minerals measured. The high values of sodium in the stem, a characteristic also reported for other submersed hydrophytes, suggest that this element has an active biological role in submersed hydrophytes. We speculate that the sodium and potassium in the stem may develop negative osmotic potential in the stem, sufficient to facilitate the movement of water and minerals from the roots to the stem, analogous to the mechanism evolved in halophytes. Calcium was the dominant mineral in the emergent floral stem, because of its structural role and slow mobilization in the phloem. Iron was the most common mineral measured in the roots, caused by root losses of oxygen and oxidizing enzymes which formed a sheath of precipitated iron on the roots.

Though $\underline{M}$. $\underline{heterophyllum}$ exhibits luxury consumption, its biological importance is probably not significant. In this study there was little evidence to support the concept that nutrient storage has a critical role

in meeting M. heterophyllum's mineral requirements during the growing season. Rather, it is suggested that the plant rapidly mobilizes minerals primarily from nutrient rich sediments to meet its nutrient needs.

III. COMPETITIVE INTERACTIONS BETWEEN

MYRIOPHYLLUM HETEROPHYLLUM,

PHYTOPLANKTON AND SEDIMENTS IN LITTORAL WATERS

Introduction

Much concern has been expressed over the proliferation of unwanted
aquatic plants, resulting from increased nutrient runoff into surface
waters. In deep lakes, fertilization typically stimulates limnetic
algal blooms. However, in shallow lakes and ponds, nutrient enrichment
to littoral waters have the potential to stimulate either phytoplankton,
periphyton or rooted macrophyte growths. There is increasing evidence
to suggest that these three types of plants actively compete with each
other for dominance. For example, field and laboratory studies indicate
that phytoplankton development is inhibited in waters supporting dense
growths of submersed macrophytes (Hasler and Jones 1949, Kimball and
Kimball 1977). Hypotheses for the cause of phytoplankton inhibition in-
clude shading (Brandl et al. 1970), secretion of organic inhibitors
(Hasler and Jones 1949), competition for nutrients, and alteration in
the ionic milieu by the photosynthetic activity of submersed macrophytes.
Conversely, Schindler and Comita (1972) reported that the elimination of
littoral phytoplankton blooms can stimulate development of submersed
macrophyte growth.

Recent studies have shown that the most important method for
attached aquatic angiosperms to obtain phosphorus is by root uptake from
sediments (Best and Mantai 1978, Gentner 1977). Therefore, attached
macrophytes may not directly compete with the phytoplankton for available
nutrients in the water column. Furthermore, senescence and decay of
hydrophytes could enrich the littoral waters with nutrients and organic
matter (Barko and Smart 1980, Carpenter 1980, Landers 1979). Much evi-
dence also suggests that the sediment – water interface can greatly
affect the fate of nutrient additions to aquatic ecosystems (Fee 1979,
Schindler et al. 1980), an interaction of considerable magnitude in the
shallow water zone.

The purposes of this study were to describe the competitive inter-
actions between submersed hydrophytes and phytoplankton, and to deter-
mine the possible pathways for pulse and continuous nutrient additions
to littoral waters. Nutrient uptake sites examined include the sediments,

phytoplankton and the submersed macrophyte - epiphyte complex. *In situ*
enclosures have been used successfully to isolate water columns for fer-
tilization experiments (Goldman 1962, Schindler 1971, Twinch and Breen
1978a, b, 1981). Consequently, similar enclosures were used to approx-
imate natural conditions for nutrient addition experiments. Implications
of chemical aquatic weed treatment on phytoplankton and nutrient levels
were also examined.

Methods

Study Sites

The study site was at Lees Mill, which is described in Section II.
Aquatic plant growth was dominated by a nearly homogeneous zone of
Myriophyllum heterophyllum Michx. growing in depths of 0.5 to 3.0 m.
Intermixed with *M. heterophyllum* stands were clumps of *Nuphar*, *Nymphea*,
Potamogeton and *Brasenia* (Figure 11). The sediments were characteristically
a soft, fine silt, interspersed with sporadic large granite boulders.

Data from Front Bay, Lake Winnipesaukee (NH Water Supply and Pollu-
tion control Commission, unpublished) was also analyzed. Front Bay
(Site 3, Figure 1) covers 12 ha, z_{max} = 4 m, and 60% of the bay's shoreline
is occupied by residential and commerical development. Until September
1977, Front Bay received the discharge from the Town of Wolfeboro's
secondary sewage treatment plant.

Chemical and Biological Methods

Subsurface water samples (0.5 m) were collected for chlorophyll *a*
and phaeophytin (Strickland and Parsons 1972), and total phosphorus (EPA
1974). Water chemistry profiles for dissolved oxygen and temperature
were measured *in situ* with a Yellow Springs Model 51B meter. *In situ*
profiles of redox potential (E_7), pH and conductivity (μmho cm^{-1}, 25°C)
were taken using a peristaltic pump to bring the samples into a surface
reservoir containing the probes, without aeration occurring. Instrumen-
tation included a Corning pH meter with an Orion Pt redox electrode,
Hach pH meter and Markson Model 10 conductivity meter. The instruments
were calibrated prior to each data collection. Light penetration was
measured with a 25 cm Secchi disc and photosynthetically available
radiation (PAR) was determined with a LiCor 185A Quantum meter (400-
700 nm, μeinsteins cm^{-2} sec^{-1}).

Figure 11. Sample site locations at Lees Mill in Lake Winnipesaukee

Qualitative sub-surface plankton samples were collected with a 60 μm net. Quantitative plankton counts were made with an inverted microscope on samples collected in a Van Dorn sampler from 0.5 m and 1 m depths and preserved in Lugols solution (Vollenweider 1969). In 1979 Chrysophaerella was mistaken for debris, because the colonies frequently burst. The problem was recognized in 1980 and the broken colonies were counted. Algae sampled while free floating were defined as phytoplankton and algae adhering to macrophytes as periphyton.

Enclosure Experiments

Nutrient additions were made to enclosures constructed within a dense stand of M. heterophyllum at 1.5 to 2.0 m. Four different experimental conditions were used: enclosures containing (a) lakewater and sediments, (b) lakewater, sediments and M. heterophyllum, (c) lakewater and rooted M. heterophyllum, but without the sediments, and (d) only lakewater. The enclosures were made of 4 mil clear polyethylene plastic using two designs (Figure 12). Enclosures without sediments had plastic bottoms, and two enclosures of this type had M. heterophyllum transplanted through small holes punctured in the plastic bottom. Tops of the enclosures were 10 - 15 cm above the lake's water level and the bottoms were weighted into the sediments. Water exchange between the enclosures and ambient lakewater was negligible. Nutrient additions consisted of phosphorus as NaH_2PO_4 and nitrogen as $NaNO_3$, in a distilled water solution dispersed across the water surface. Herbicide treatment was with Silvex (2,4,5-TP). The experimental design and fertilization rates are described in Table 9 and Figure 13. Chlorophyll a, total phosphorus, temperature, dissolved oxygen, pH, conductivity, redox potential, and PAR were monitored in M. heterophyllum weed beds (sites 19 - 23), the limnetic zone (sites 31 and 32) from July 1977 to October 1979, and in the enclosures during the summer (Figures 11, 13).

In Situ Light Inhibition Experiment

The effects of shading by M. heterophyllum on fertilized phytoplankton populations were tested. One liter of water from the 1979 nitrogen plus phosphorus fertilized enclosure experiencing an algal bloom dominated by Ankistrodesmus was collected and mixed with 4 1 of surface

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Figure 12. Experimental Enclosure Design
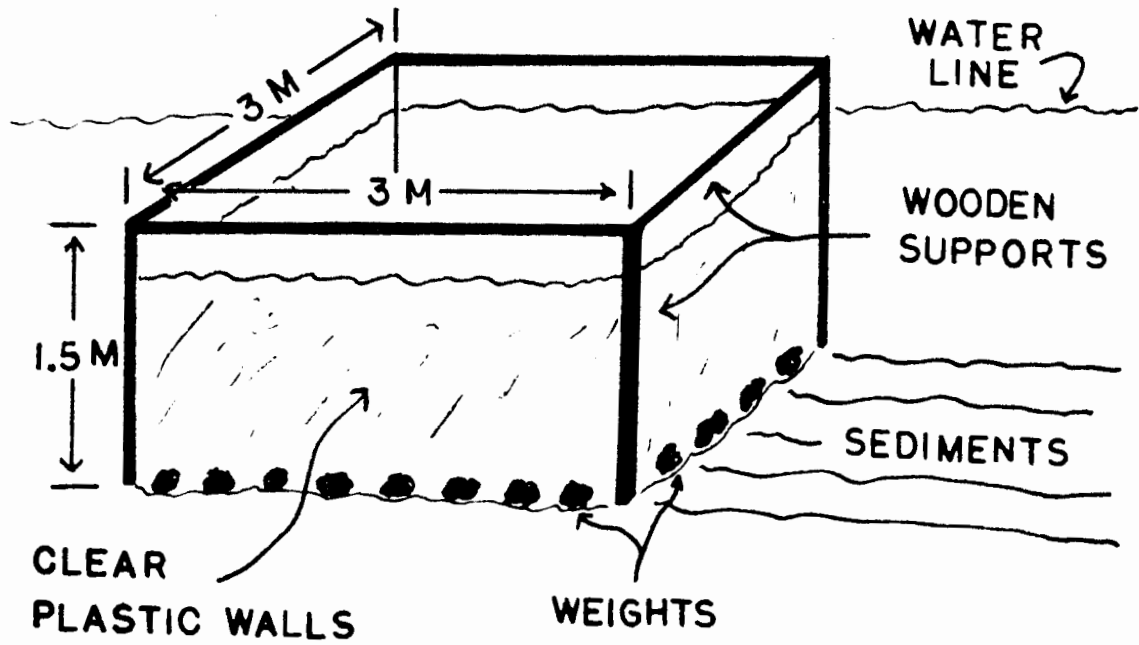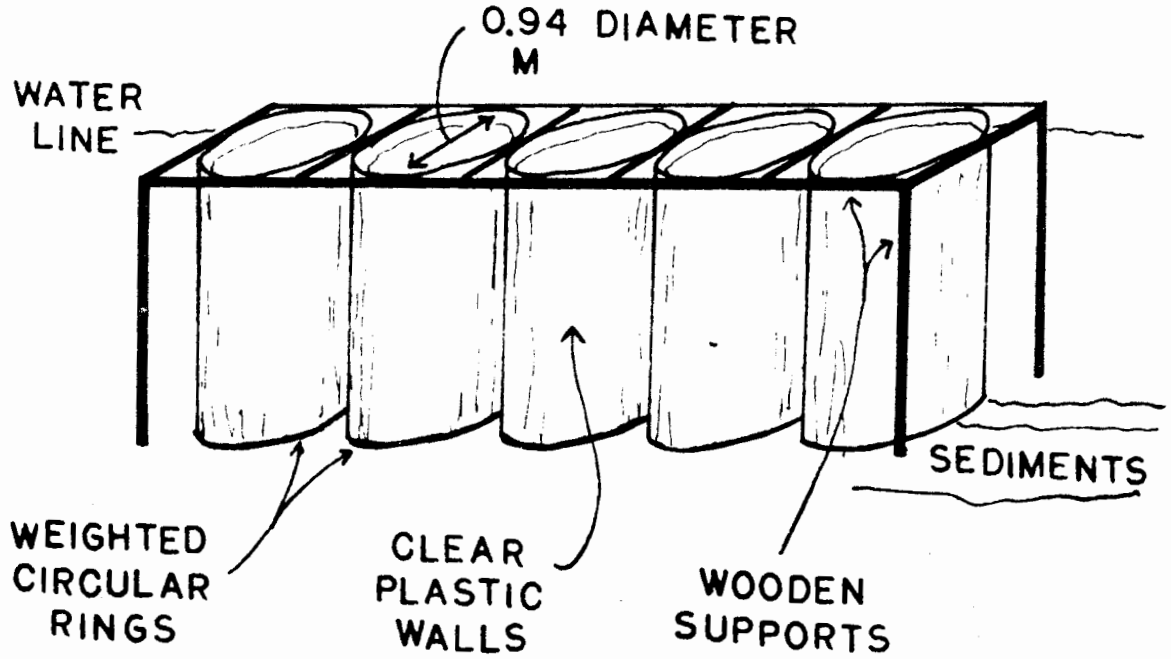
Figure 13. Field lay-out for 1977 - 1979 nutrient addition experiments

1977
0.7 m² CYLINDERS WITHOUT M. HETEROPHYLLUM
AND 9 m² ENCLOSURE WITH M. HETEROPHYLLUM
C= CONTROL.   N,P= NUTRIENT ADDITIONS

1978
9 m² ENCLOSURES WITH M. HETEROPHYLLUM
S= 2,4,5-TP TREATMENT

1979
9 m² ENCLOSURES WITHOUT SEDIMENTS OR
M. HETEROPHYLLUM
C/N= CONTROL, THEN N ADDITION
C/NP+Mh= CONTROL, THEN M. HETEROPHYLLUM TRANSPLANT PLUS
N,P ADDITIONS

30 m
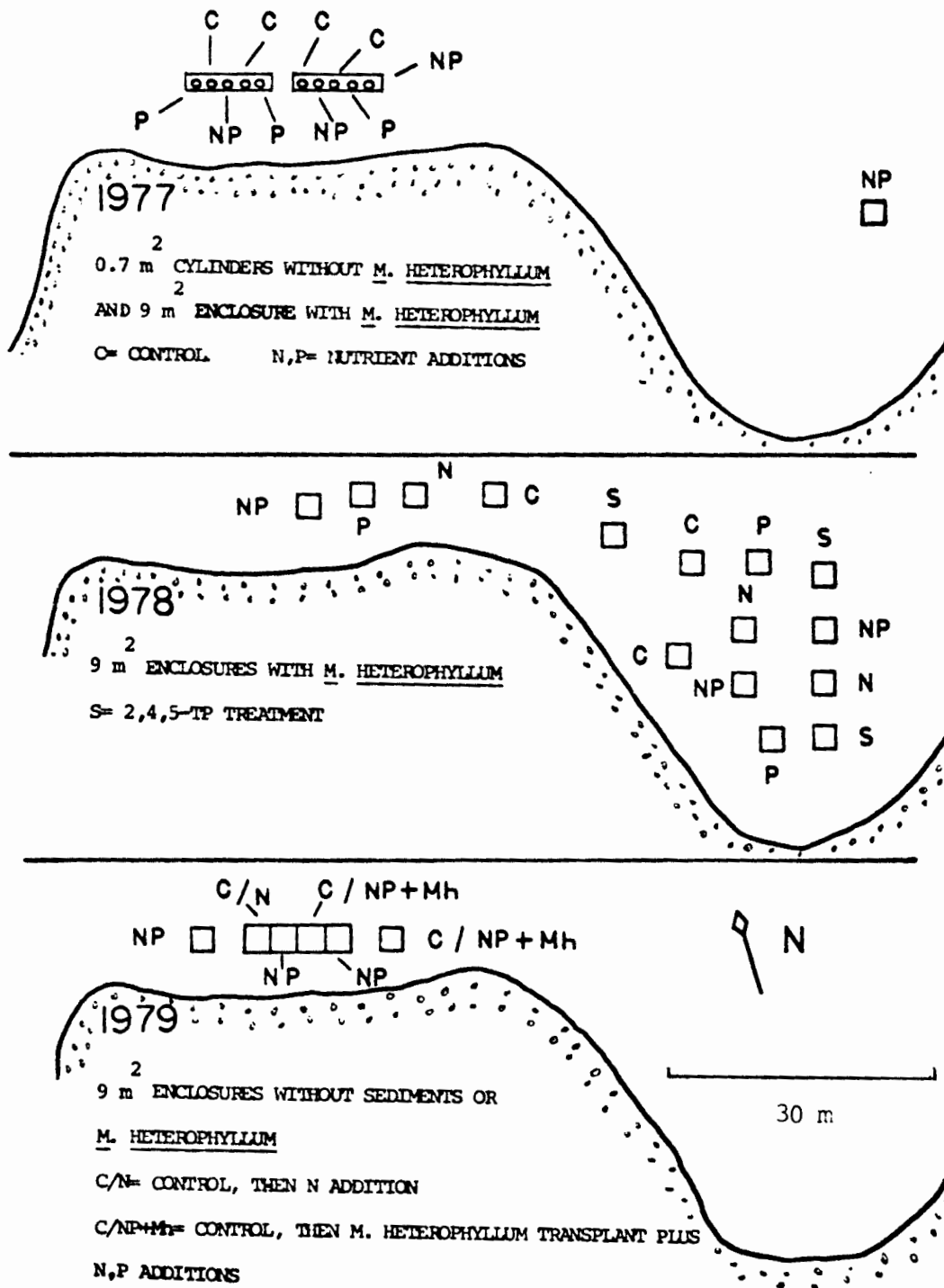
Table 9 .   1977 – 1979 Nutrient Addition Experiments

Year	Enclosure Design	Volume (m^3)	# Built	Treatments (# Enclosures)	Contents of Enclosure	Date of Enclosure Construction	Dates of Nutrient Additions
1977	0.7 m diam. cylinders	1.03	10	Controls = 4 +P = 3 +NP = 3	Lakewater & Sediments	17-VII	16 mg P, 0.21 g N (3-VIII, 10-VIII, 16-VIII, 23-VIII, 6-IX) 32 mg P, 0.42 g N (18-IX, 2-X, 16-X, 3-XI, 25-XI)
1977	3 m x 3 m enclosure	13.7	1	+NP = 1	Lakewater & Sediments & M. heterophyllum	17-VII	205 mg P, 2.74 g N (3-VIII, 10-VIII, 16-VIII, 23-VIII, 6-IX) 410 mg P, 5.47 g N (18-IX, 2-X, 16-X, 3-XI, 25-XI)
1978	3 m x 3 m enclosure	17.0	15	Controls = 3 +P = 3 +NP = 3 +N = 3 +2,4,5-TP = 3	Lakewater & Sediments & M. heterophyllum	25-VI	255 mg P, 3.4 g N (7-VII, 14-VII, 20-VII) 510 mg P, 6.8 g N (13-VIII, 22-VIII, 30-VIII, 8-IX, 16-IX) 2,4,5-TP (BEE) at 1 mg/l (13-VIII)
1979	2.4 m x 2.4 m enclosure	10.9	6	Controls=3, +NP=3 then 2 controls received M. heterophyllum transplants +NP and 1 control received only +N	a. Lakewater or b. Lakewater & M. heterophyllum (planted through plastic bottom)	23-VI	330 mg P, 4.35 g N (2-VII, 9-VII, 18-VII, 1-VIII, 8-VII, 2-IX, 8-IX) 650 mg P, 8.70 g N (15-VIII, 21-VIII) Milfoil transplant: 25-VII

littoral waters on 1-VIII-79. The combined 5 1 of water received 2 mg nitrogen as KNO_3 and 150 µg of phosphorus as KH_2PO_4, were agitated and then dispensed into twenty-four 125 ml BOD bottles. The chlorophyll a and total phosphorus concentrations were 13 and 50 µg 1^{-1}, respectively. The bottles were suspended vertically in (a) a dense growth of M. heterophyllum and (b) an adjacent area cleared of M. heterophyllum. At each site, 3 pairs of bottles were incubated immediately below the water surface and 3 pairs at 1 m. Seven days later the bottles were harvested, paired bottles combined, and their content analyzed for chlorophyll a. One set of paired bottles at the 0 and 1 m depths in the M. heterophyllum stand were lost.

In Vitro Herbicide Experiment

The influence of M. heterophyllum decay induced by herbicide application on phosphorus levels in the water was examined. Fine, organic sediments and M. heterophyllum sprigs were collected on 10-XII-79 from Lees Mill. In six 35 1 aquaria, 25 M. heterophyllum 20 cm sprigs were rooted in 2 - 4 cm of sediment and tap water on 15-XII-79. The estimated biomass was 320 g dry wt m^{-2}. The aquaria were kept at 15 - 21°C in indirect sunlight. On 5-II-80, 2,4,5-TP was applied at 2 mg 1^{-1}. Temperature, dissolved oxygen, pH, redox potential, conductivity, and total phosphorus were measured at the surface and 25 cm depth 6 times until termination of the experiment on 16-III-80.

In Vitro Sediment Experiments

The ability of hydrosoils to sorb or release phosphorus was tested. Fine, organic muds were collected from weed beds at Lees Mill with an Ekman dredge, and stored in the dark at 4°C with 1 - 5 cm of water. A 50 ml volume of wet mud was covered with 200 ml of distilled water or 200 ml of a 100 µg P 1^{-1} (NaH_2PO_4) solution in acid washed 250 ml Erlenmeyer flasks, kept for 3 or 7 days in the dark at 15-21°C and then analyzed for total phosphorus. All treatments were run in triplicate. Controls were identical treatments, but without the sediments. Dissolved oxygen, conductivity and pH of the water were measured before and at the termination of one 7 day experiment.

The effect of water circulation on hydrosoil phosphorus sorption and release was also examined. Erlenmeyer flasks with fine, organic

silts from Lees Mill were prepared as described above, except that lake-
water was used. Controls were lakewater, 5 flasks agitated and 5 flasks
not agitated. Treatments were five flasks of lakewater with muds agita-
ted and 5 identical flasks without agitation. Agitation was applied by
a shaking table at a speed just insufficient to resuspend the sediments
into the overlying water. The experiment was run for 21 days, with agi-
tation applied for 8 hrs day^{-1}. Total phosphorus in the water was measured
at the end of the experiment.

Results

Physio-chemical Characteristics of the Study Site

Lake Winnipesaukee's water level is controlled by a dam and fluctu-
ates about 1 m annually. Minimal levels are maintained during the winter
through spring to reduce shoreline damage by ice movement and for down-
stream flood control. Maximum water levels occur during May - June,
followed by a continuous decline. Monthly precipitation is constant for
much of the year, but unusually heavy rains can rapidly raise the lake
level 10 - 20 cm as in the autumn of 1977 (Figure 14). Thermal stratifi-
cation was absent in the littoral zone, but present in the limnetic
waters during the summer. During July and August, water temperatures
frequently reached $30^{o}C$ (Figure 15). Littoral zone mid-day pH values
were acidic during the winter and basic during much of the growing season.
Depth profiles of pH during the summer, when M. heterophyllum
reached the surface, were characterized by surface to mid-depth (0.5 - 1.5 m)
maxima (Figure 16), caused by photosynthetic activity. In the limnetic waters,
maximum summer pH values were comparatively lower and maximum at the
surface. Midday dissolved oxygen levels frequently exceeded 100% saturation
in dense M. heterophyllum stands during the summer due to photosynthesis.
During the non-growing season, dissolved oxygen levels approximated
100% saturation for the water temperature (Fig. 17). Anaerobic conditions
were absent at all depths in the littoral waters and the redox potential
(E_7) was typically 300 - 400 mv. Below 3 m, oxygen levels were less than
4 mg l^{-1} during summer stratification in the limnetic station. The 1%
compensation point for PAR was approximately 4 m depth during the summer in
the limnetic waters.

Figure 14. Moultonboro lake level and precipitation data for Lake Winnipesaukee (USGS)
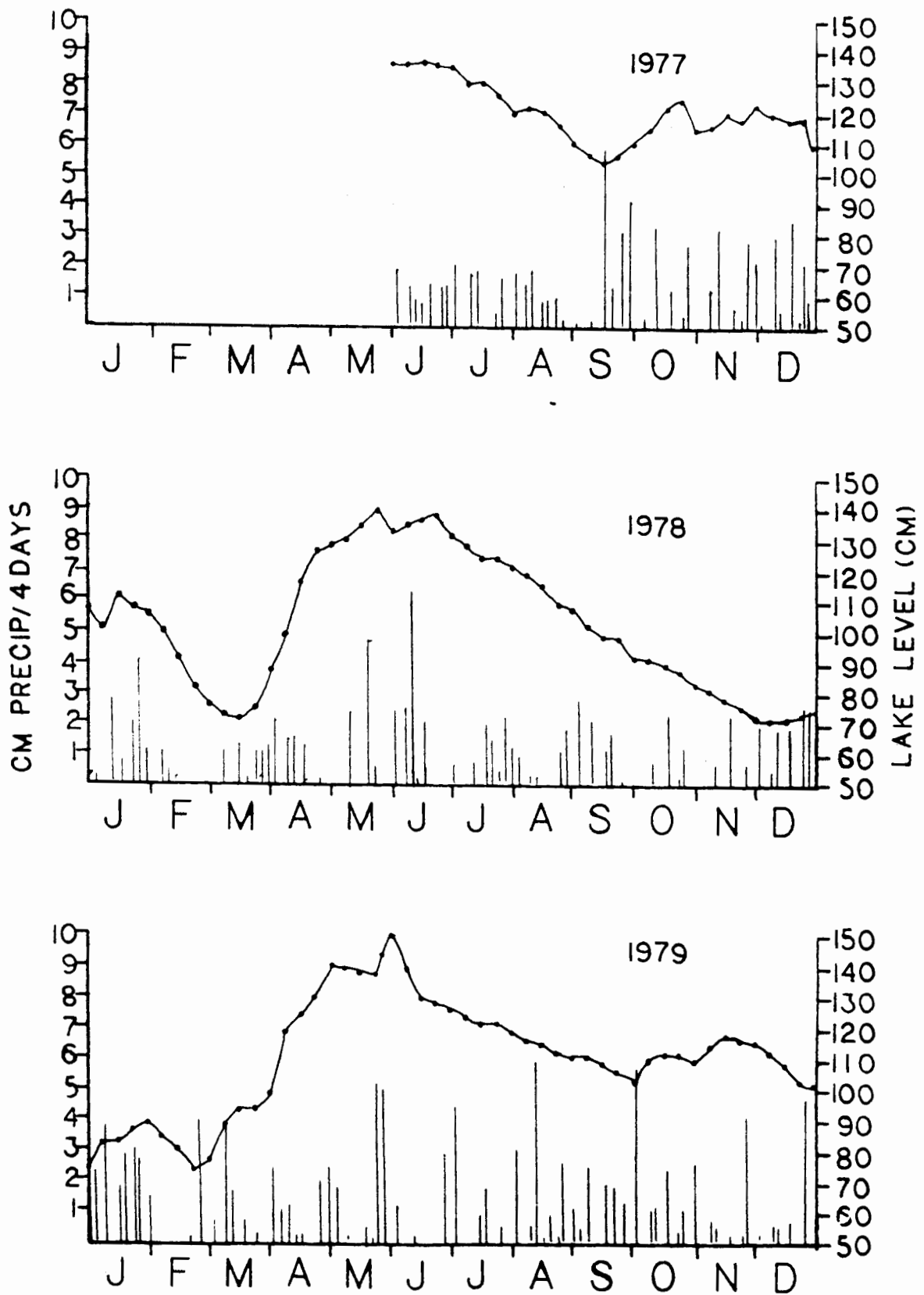
Figure 15. Temperature isopleths for the littoral sample site
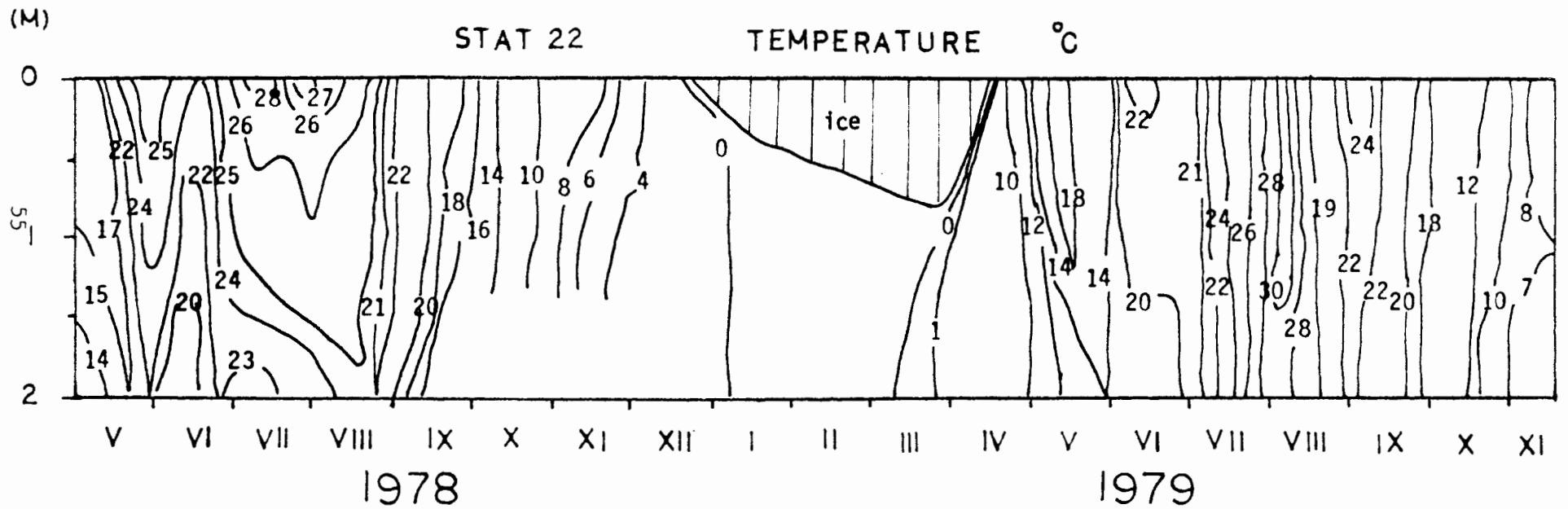
Figure 16. pH isopleths for the littoral sample site
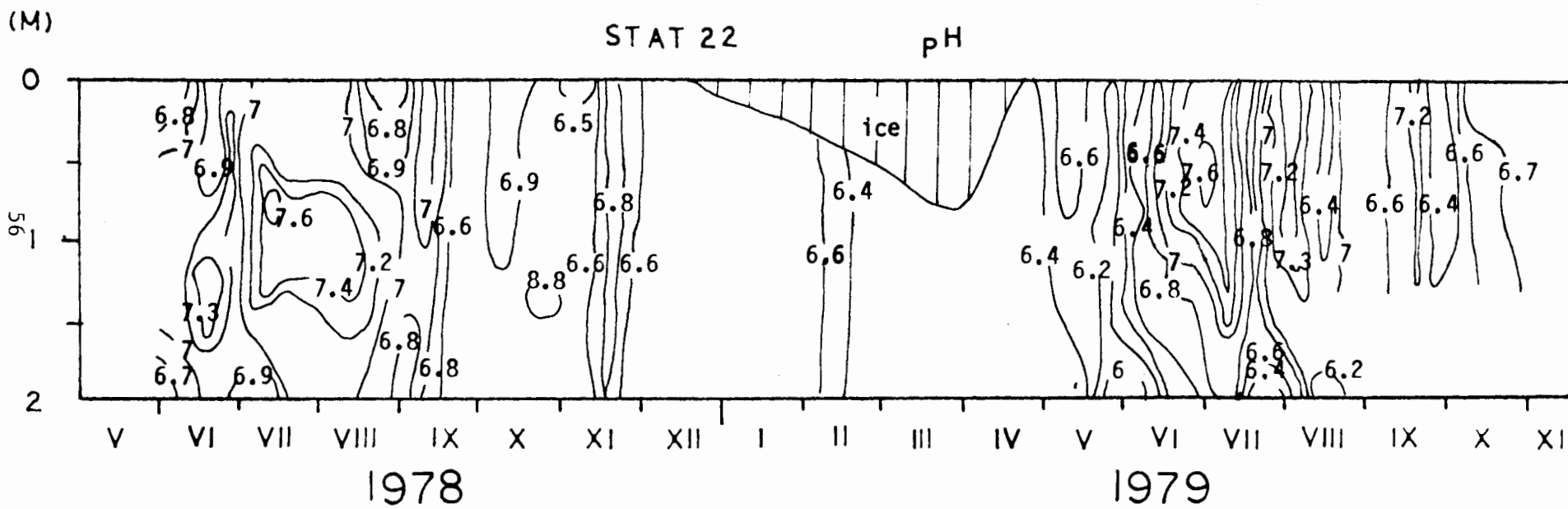
Figure 17. Dissolved oxygen isopleths for the littoral sample site
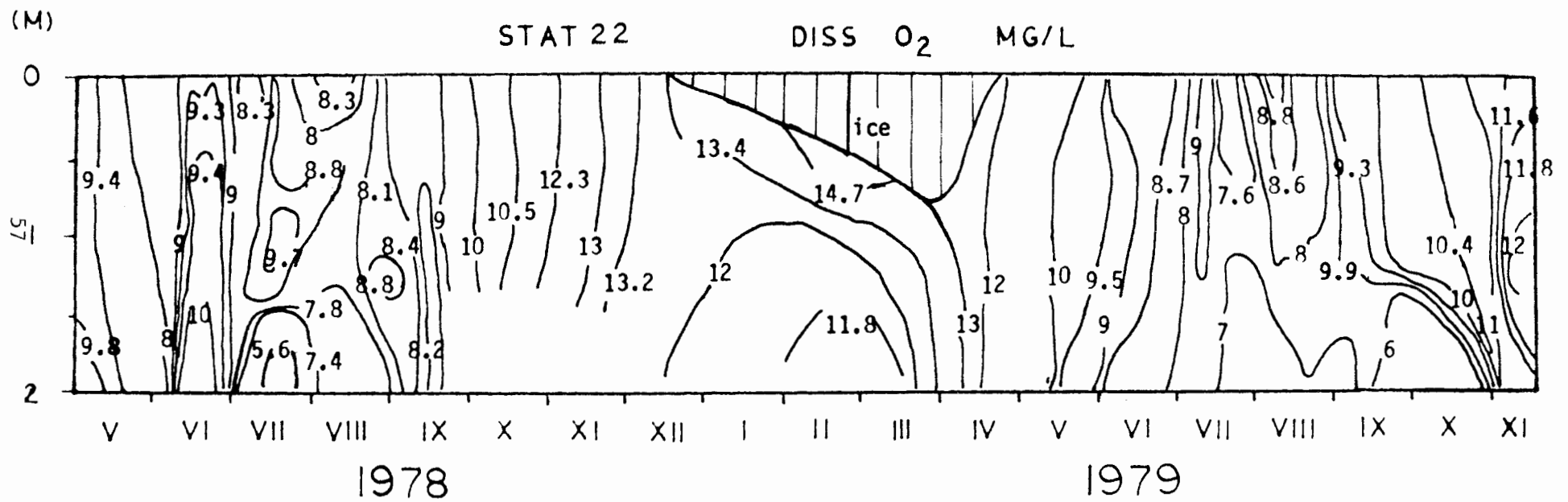
Specific conductance ranged from 40 to 75 μmho cm^{-1}, 25°C and no seasonal trends were apparent. Alkalinity and calcium levels were 7 mg l^{-1} CaCO$_3$ and 3 - 5 mg l^{-1}, respectively. The total phosphorus concentrations in the littoral zone were generally between 10 - 20 mg P m^{-3}. Maximum levels occurred during late summer - autumn, when they exceeded 20 mg P m^{-3} and paralleled increased algal growths (Figure 18). The total phosphorus concentrations were usually 1 - 3 mg m^{-3} larger than limnetic sample sites (Figure 19).

Littoral Phytoplankton

The littoral phytoplankton populations changed both quantitatively and qualitatively with season. During winter through late spring, the chlorophyll a values were lowest. Summer values were higher, but generally less than 5 mg m^{-3} (Figure 18), and cell counts were typically less than 1000 phytoplankton ml^{-1} (Figure 20). Similar trends occurred in the limnetic zone. Late summer to autumn peaks in the phytoplankton were common, with chlorophyll a reaching 15 mg m^{-3}. However, algal blooms were not measured in the limnetic zone. Littoral and limnetic phytoplankton species composition and density usually did not differ during the summer, but when significant differences occurred, the littoral sample sites also differed significantly between themselves. Plankton samples collected at 0.5 and 1 m depths were usually similar at both the limnetic and littoral zone (Appendices 5, 6).

Diatoms, particularly Asterionella, Tabellaria, Melosira and Eunotia, dominated the littoral phytoplankton during September through May. From May until September, the Chrysophytes, Chrysophaerella and Dinobryon were major components of the phytoplankton community. From late June through September, both Chlorophytes and Cyanophytes were prominent, including Eudorina, Staurastrum, Anabaena, Aphanocapsa, Coelosphaerium, Lyngbya, Merosmopedia, Oscillatoria and Gloeotrichia. Oedogonium, a common periphyton, was sampled in July and August, while Cryptomonas was frequent during the summer. The progressive change from diatoms, to golden-browns, then greens and blue-greens from spring through summer was similarly observed at the limnetic site.
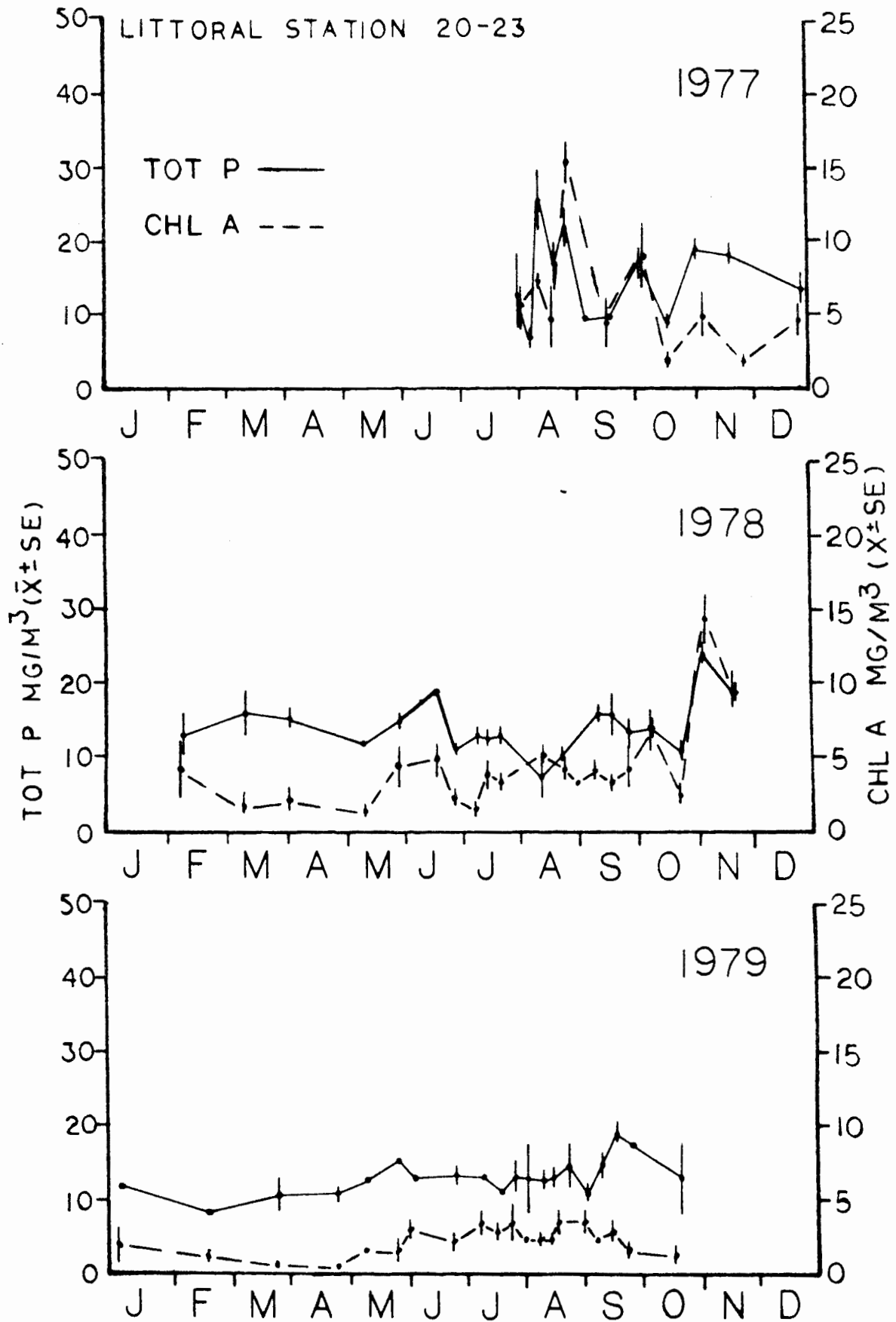
Figure 18. Total P and Chlorophyll a during 1977 - 1979 for the littoral sample sites

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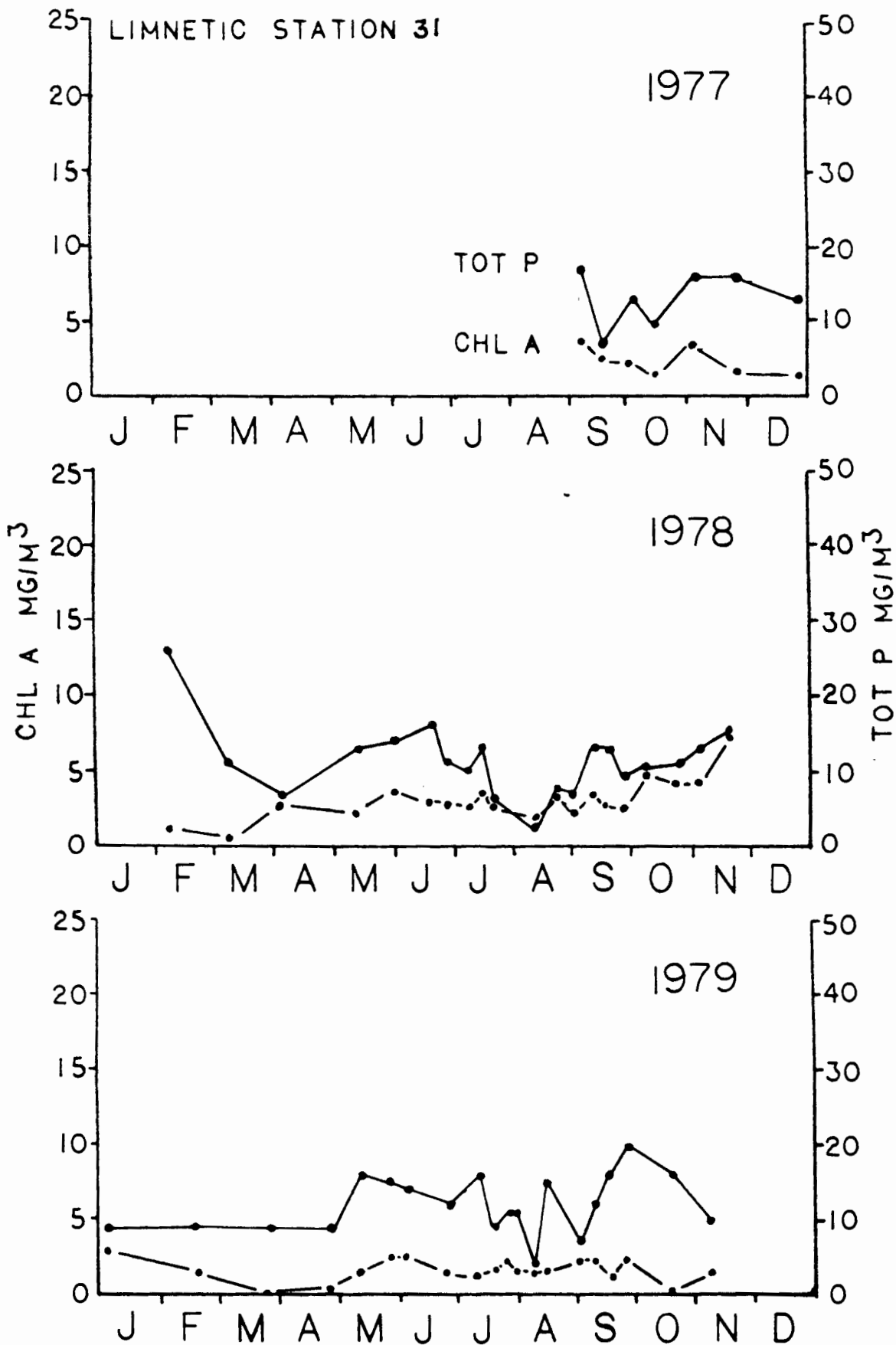
Figure 19. Total P and Chlorophyll a levels during 1977-1979 for the limnetic sample site

Figure 20. June – August 1979 phytoplankton counts for the limnetic and littoral sample sites
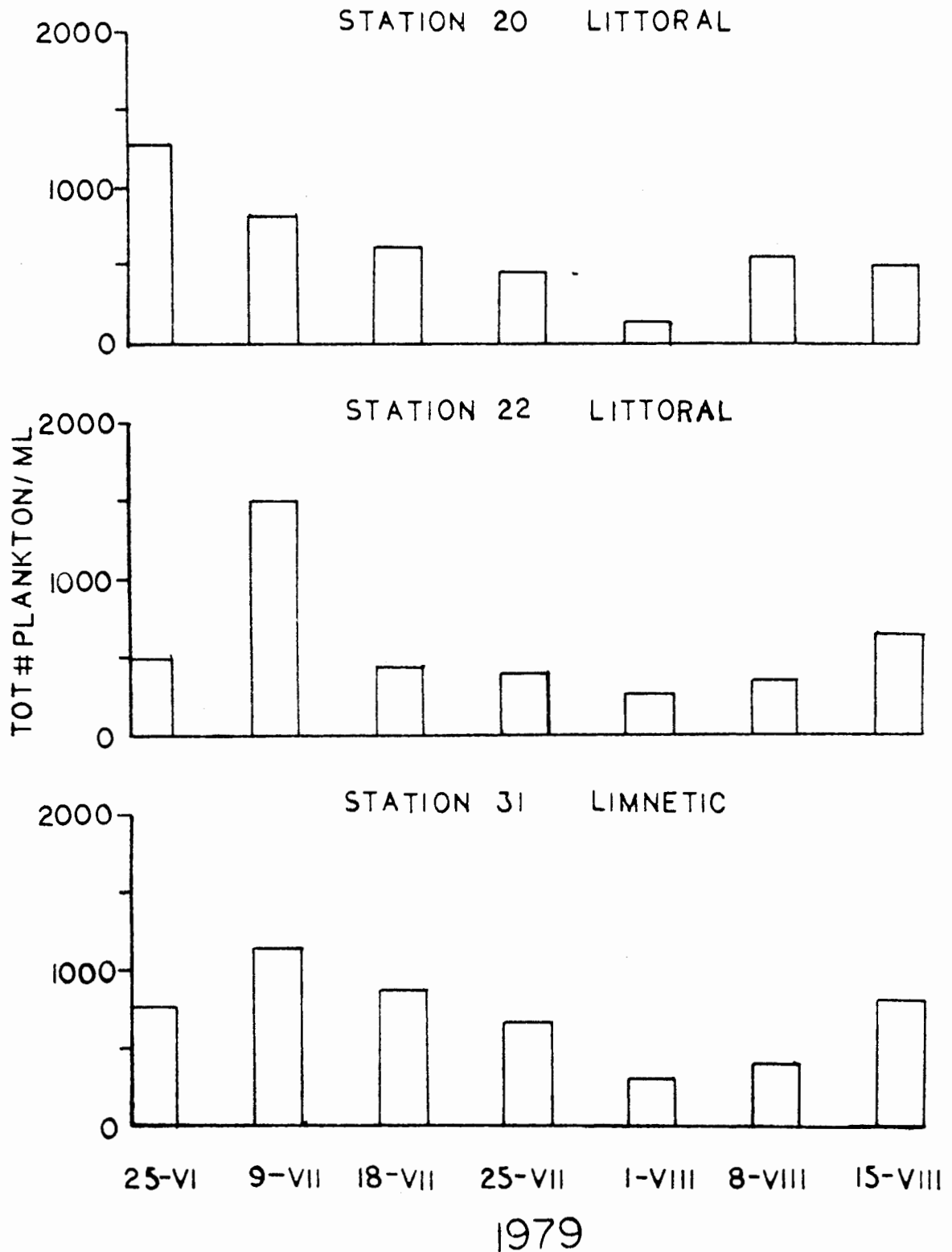
Littoral Phytoplankton PAR and In Situ Light Inhibition Experiment

Light absorbance was enhanced by naturally occurring humic substances (Secchi disc 3.5 - 4.0 m). From 0 - 0.6 m, mid-day PAR levels were similar between the littoral and limnetic sites (Figure 21). Below 0.6 m, Myriophyllum heterophyllum interfered with accurate light measurements in the littoral zone. Phytoplankton chlorophyll $\underline{a}$ concentrations in BOD bottles, following innoculation, fertilization and 7 days incubation in situ, were higher in the M. heterophyllum stands at the surface and 1 m depths, than in the open water at the surface and 1 m. Mean values $(\overline{X} + SE)$ were 27.9 ± 0.3, 18.5 ± 2.2, 16.9 ± 1.2 and 15.7 ± 1.5 mg chlorophyll $\underline{a}$ m^{-3}, respectively. The shading effect of submersed macrophytes on light levels fluctuated due to the movement of stems by wind and wave action, which diminished destructive photo-oxidative processes at the surface during mid-summer.

Nutrient Addition Experiments

Pulse additions of phosphorus and nitrogen plus phosphorus in 1977 to cylinders containing lake water and sediments were rapidly lost from the water column. Each of the first five nutrient additions had the potential to increase the total phosphorus levels by 100%, and the last four fertilizations by 200%. However, comparisons of the total phosphorus and chlorophyll $\underline{a}$ levels in the cylinders receiving fertilizations and control cylinders were not significantly different (Appendix 7), and their temporal fluctuations were in synchrony (Figure 22). The 1977 enclosure (9 m^2) with M. heterophyllum, lakewater and sediments receiving nitrogen plus phosphorus fertilizations had higher total phosphorus and chlorophyll $\underline{a}$ concentrations, compared to the cylinders. However, the enclosures' total phosphorus concentrations were considerably lower than predicted from the quantity of phosphorus added.

The results of nitrogen, phosphorus and nitrogen plus phosphorus fertilizations in 1978 to enclosures containing M. heterophyllum, lakewater and sediments were similar to the 1977 results. Although the first two nutrient additions should have increased the nitrogen and phosphorus levels 100%, and the last five fertilizations by 200%, control enclosures did not differ significantly from fertilized enclosures in total phosphorus and chlorophyll $\underline{a}$ (Figure 23, Appendix 8), or dissolved oxygen and pH. However, the M. heterophyllum foliage in all enclosures receiving

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Figure 21. Photosynthetically available radiation at 0.6 m depth for the littoral sample sites

LITTORAL STATIONS % SURFACE PAR AT 0.6M

$(\bar{X} \pm SE)$
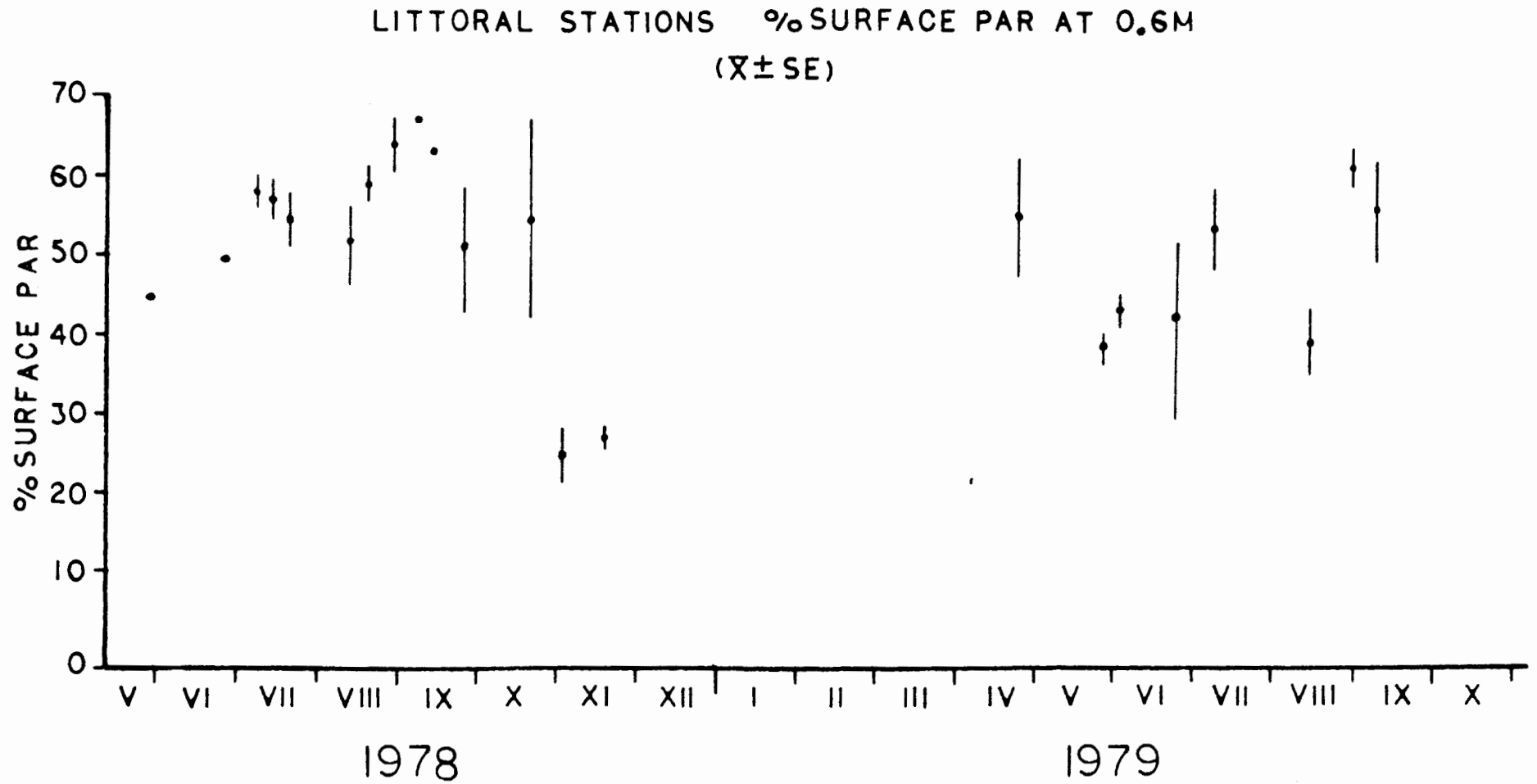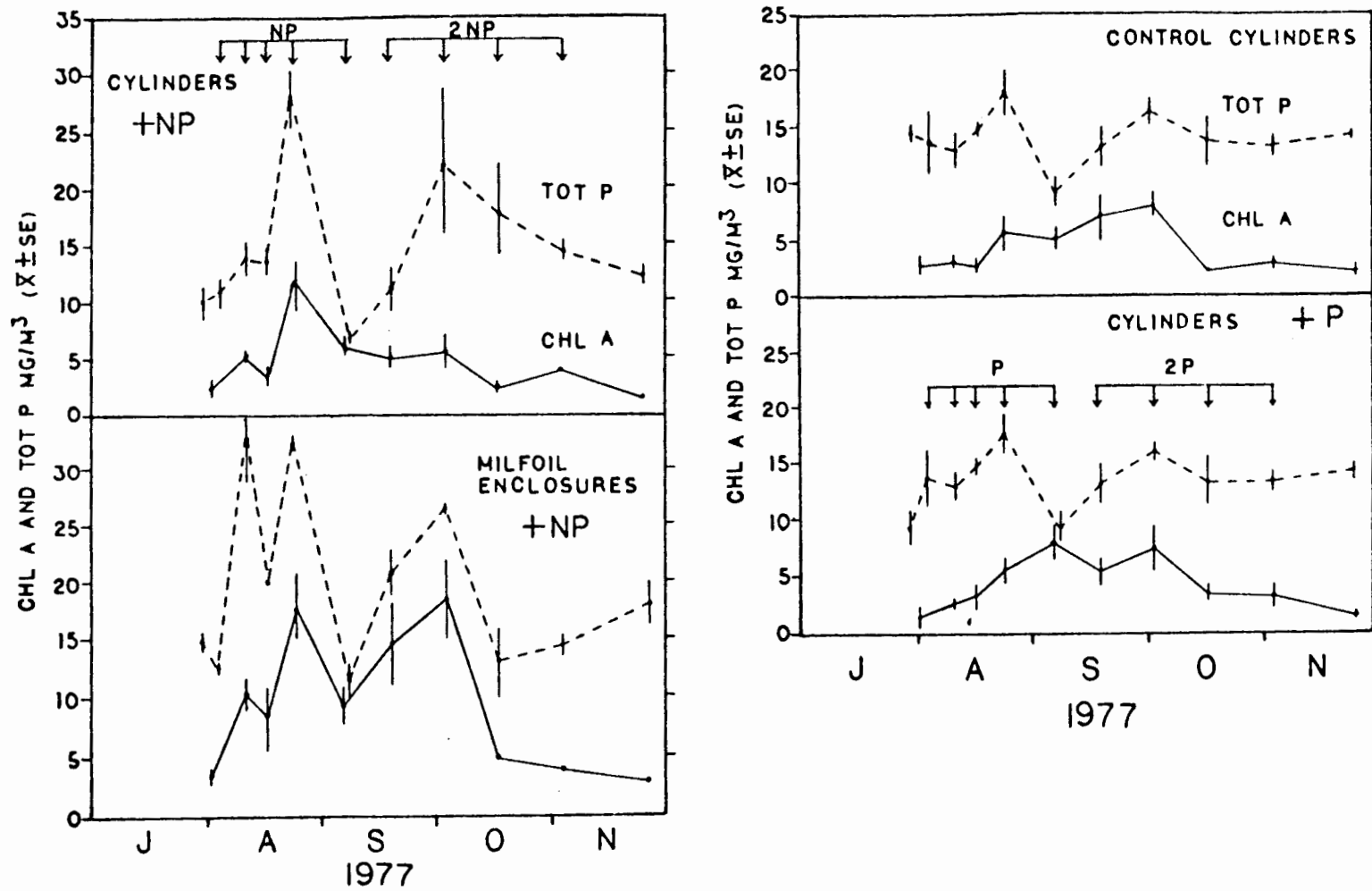
Figure 22. Total P and chlorophyll a levels in the 1977 enclosures and cylinders
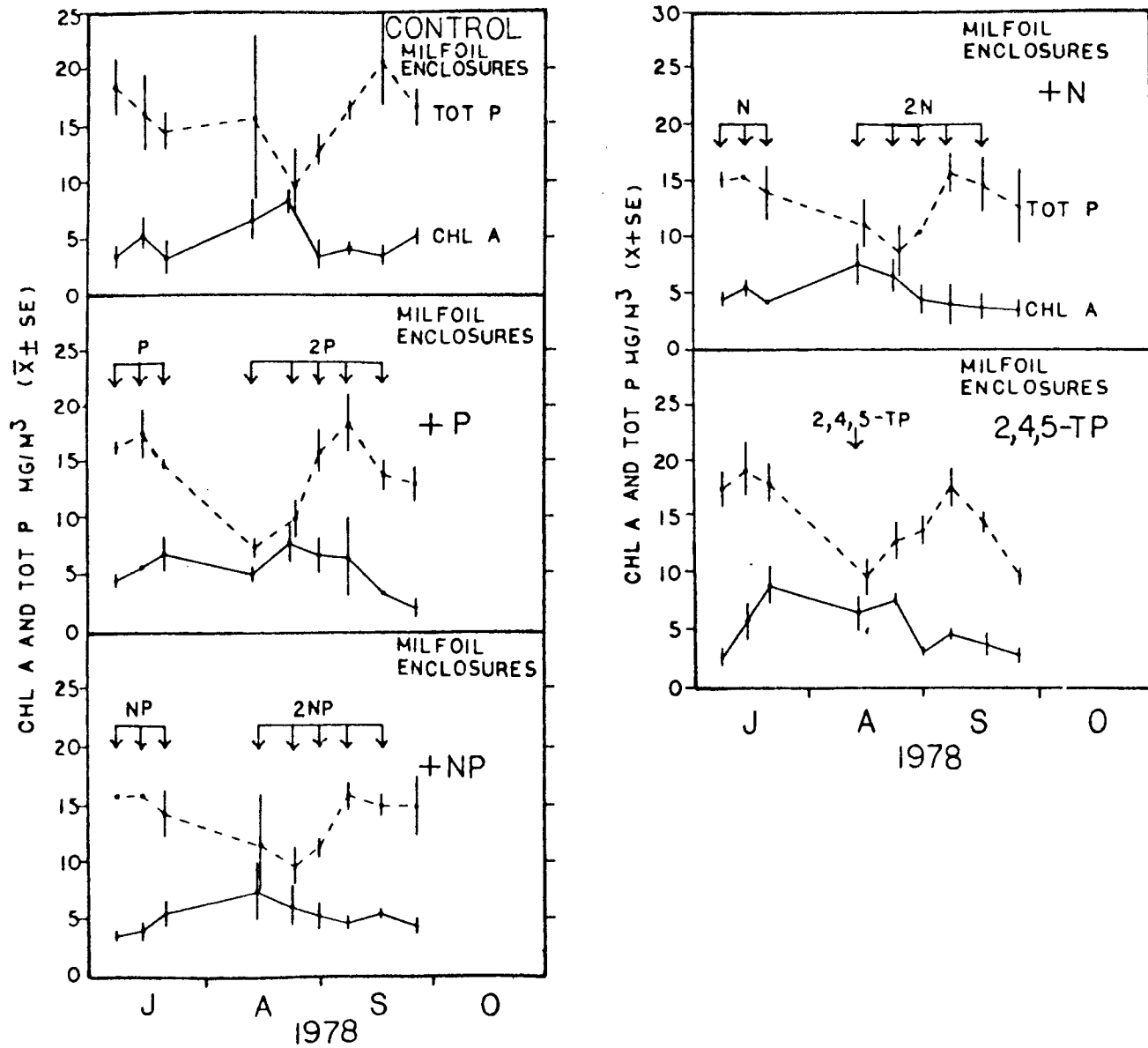
Figure 23. Total P and chlorophyll a levels in the 1978 enclosures
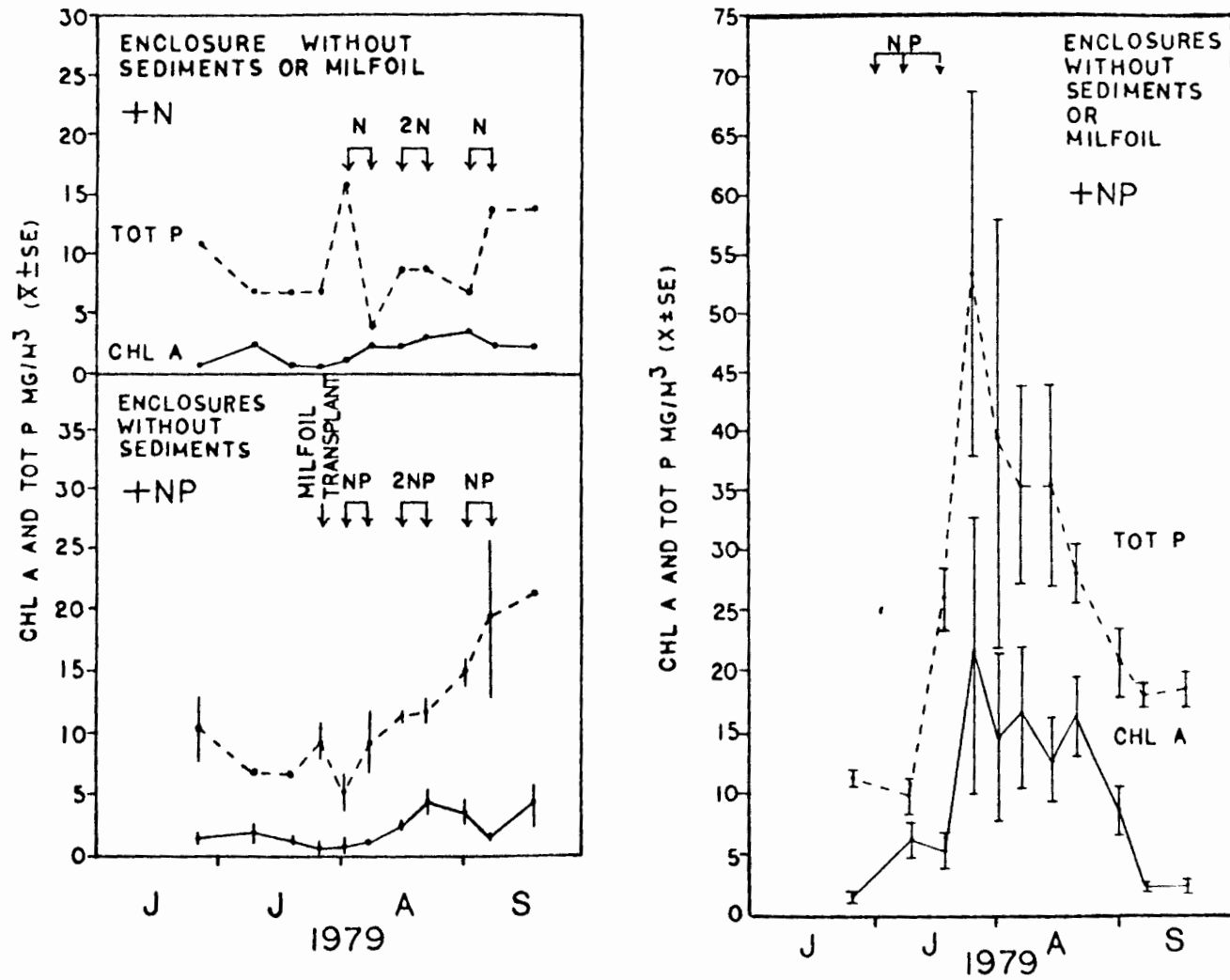
Figure 24. Total P and chlorophyll a levels in the 1979 enclosures

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phosphorus additions was covered with considerable periphyton. A die-off of the M. heterophyllum occurred in the 2,4,5-TP treated enclosures, but post-treatment changes in chlorophyll a or water chemistry were not observed, with the exception of a temporary decline in dissolved oxygen concentrations. The 1977 and 1978 stands isolated in the enclosures had increased dissolved oxygen and pH levels compared to ambient growths (Figures 25, 26), whether or not the enclosures had received fertilizations. Enclosure dissolved oxygen and pH maximum levels were 135% saturation and 9.3, respectively.

A test in 1979 to determine whether fertilizations to enclosures containing just lakewater were capable of enhancing total phosphorus and chlorophyll a levels was affirmative (Figure 24). Three additions of nitrogen and phosphorus to increase ambient lakewater levels by 200% per fertilization resulted in sudden blooms of Ankistrodesmus in enclosure 1, Gleocapsa and Eudorina in enclosure 2, and Gleocapsa, Aphanocapsa and Coelosphaerium in enclosure 3, and greatly elevated the total phosphorus concentrations of the enclosured lakewater.

Large variations in total phosphorus and chlorophyll a were observed in the nitrogen plus phosphorus fertilized enclosures (Figure 24) because accurate sampling of the algal blooms that formed floating green masses on the surface for several weeks was difficult. Additions of nitrogen to an enclosure without sediments or M. heterophyllum did not stimulate algal growth, nor did six nitrogen plus phosphorus fertilizations to two enclosures with lake water, rooted M. heterophyllum but without sediments (Figure 24). In the latter treatment, the plants were covered by considerable periphyton. The dissolved oxygen and pH levels reached 161% saturation and 10.1, respectively in the nitrogen plus phosphorus fertilized enclosures sustaining algal blooms (Figure 27). The fertilized enclosures without M. heterophyllum or sediments had significantly higher total phosphorus and chlorophyll a levels as compared to other 1979 treatments (Appendix 9).

Front Bay, Lake Winnipesaukee, received continuous phosphorus input from the town of Wolfeboro's secondary sewage treatment plant until 1977, when the effluent was diverted to a forest spray irrigation system. Nutrient loading rates prior to diversion were highest during the summer, when water flow from the Smith River tributary was minimal and the town's population increased tenfold with tourists. Major algal blooms occurred annually during the ice free season and the water was extremely turbid.

Figure 25. Dissolved oxygen and pH levels in the enclosures, cylinders and ambient M. heterophyllum growths - 1977
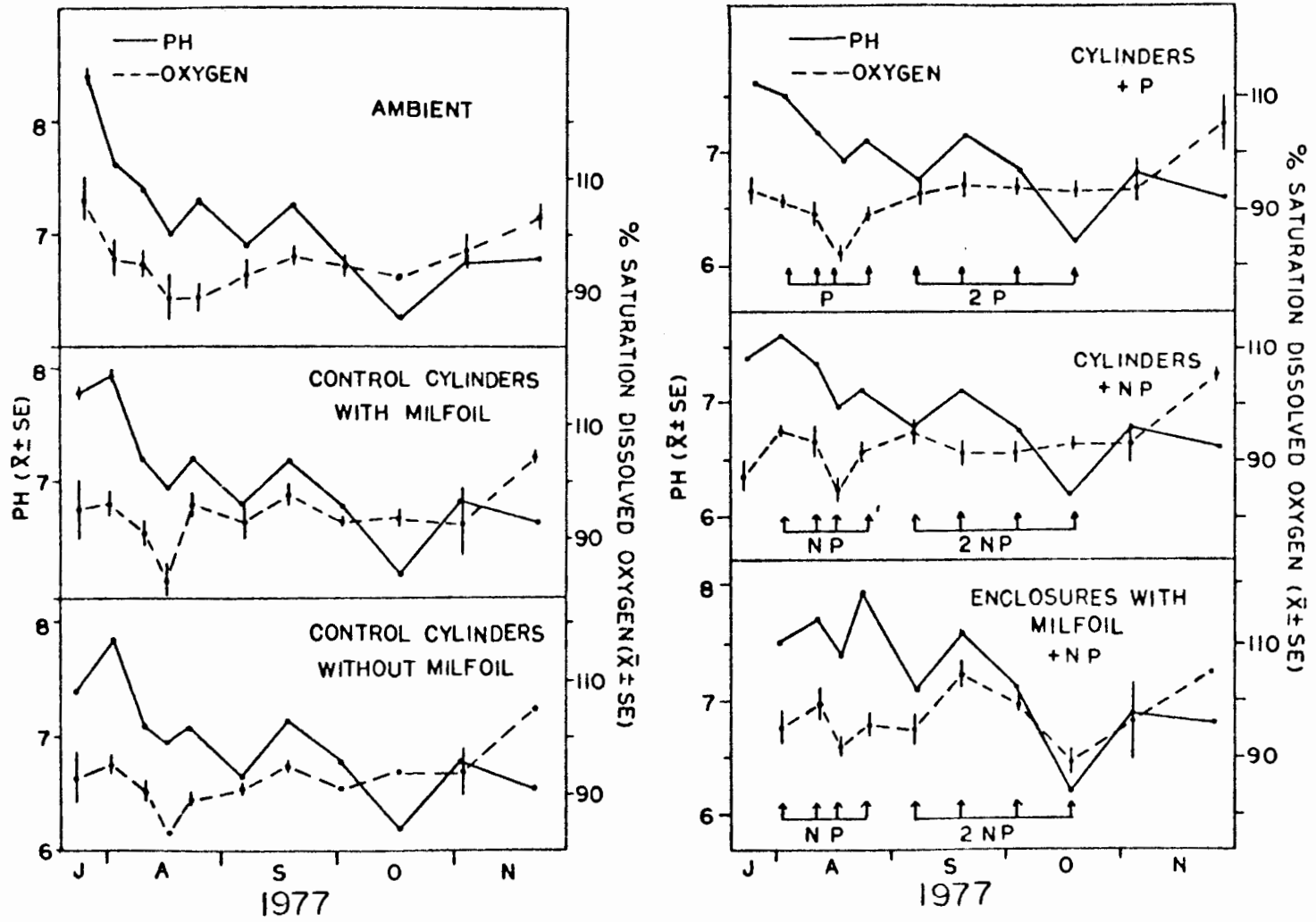
Figure 26. Dissolved oxygen and pH levels in the enclosures and ambient M. heterophyllum growths - 1978
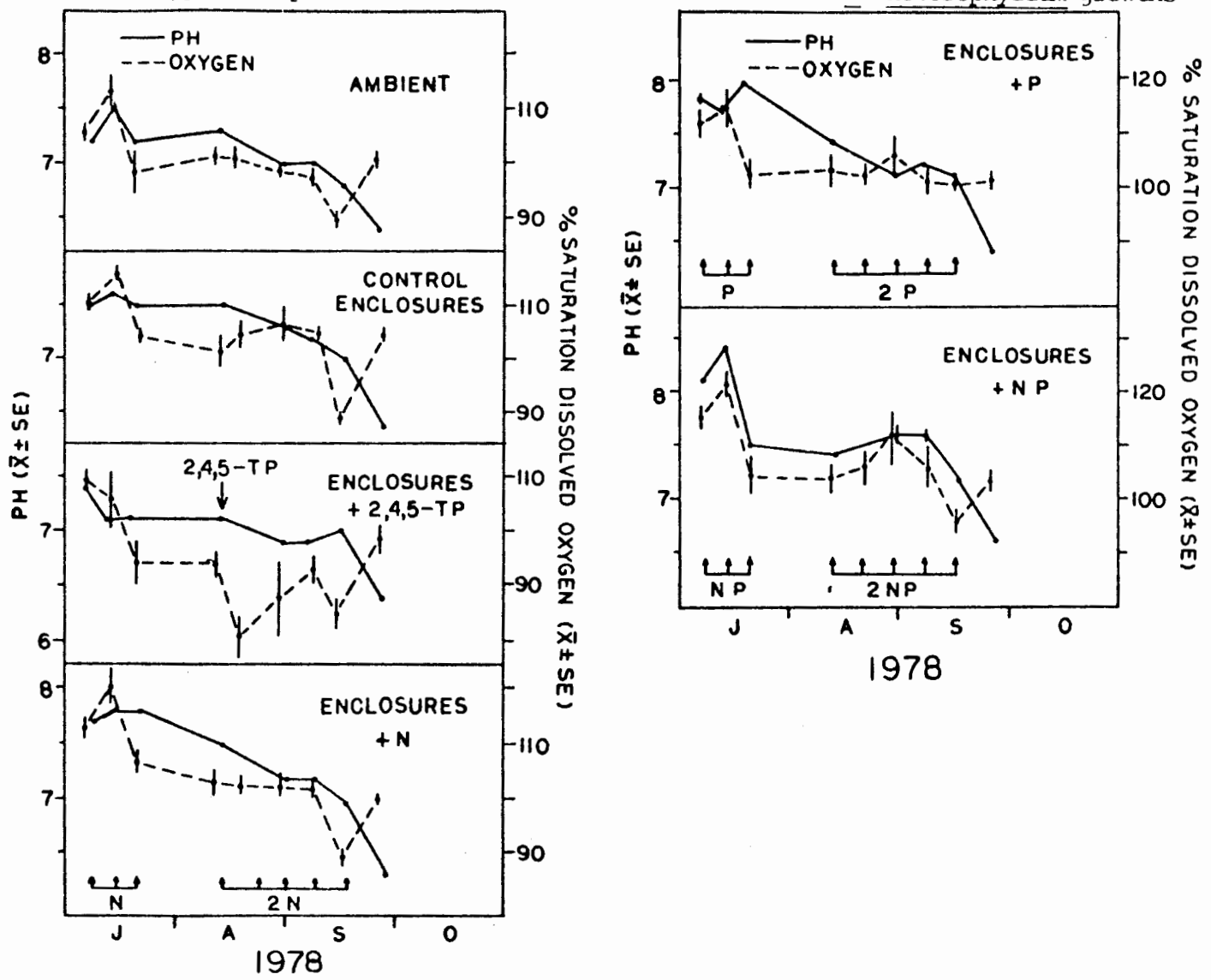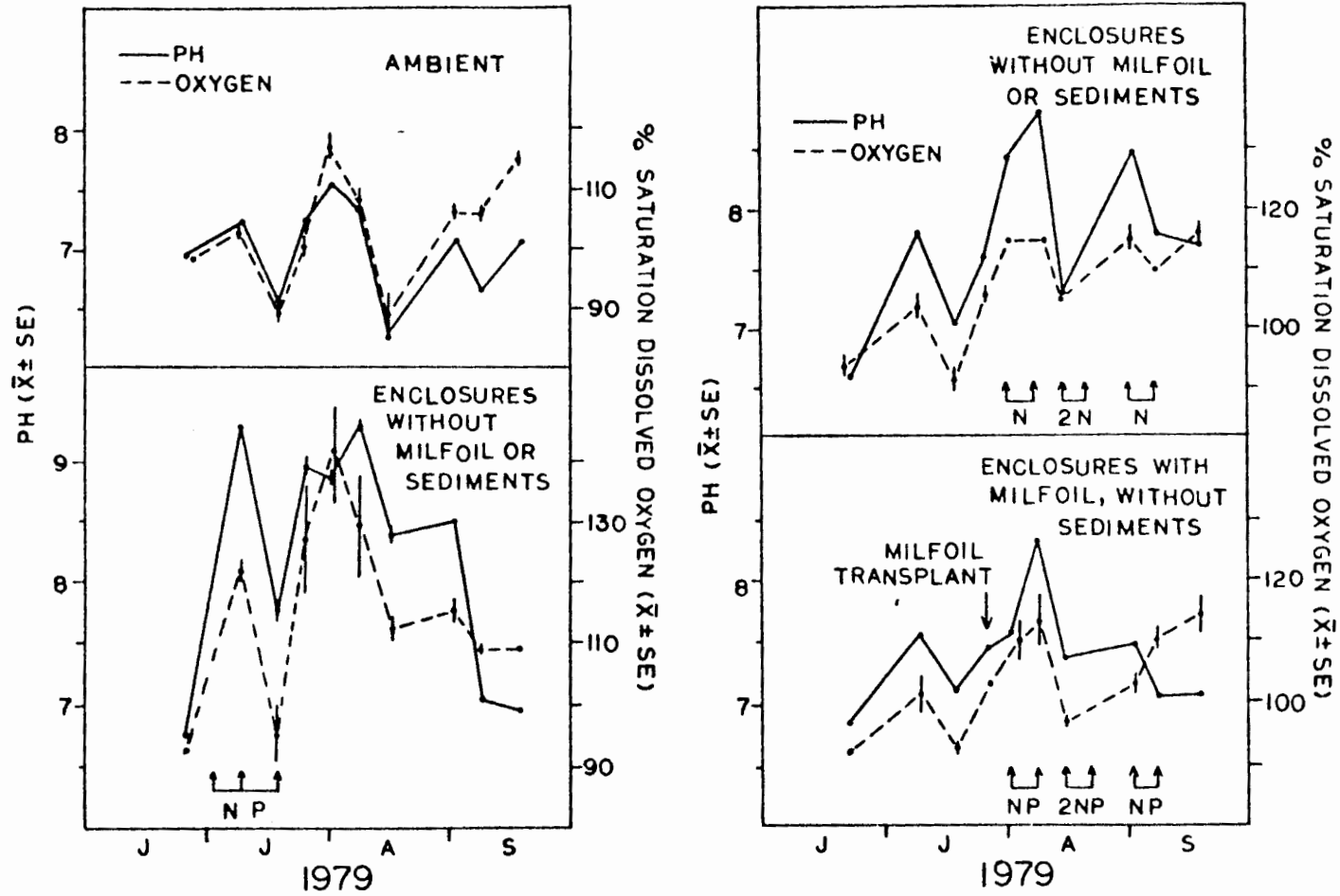
Figure 27. Dissolved oxygen and pH levels in the enclosures and ambient M. heterophyllum growths - 1979

During the 1978 spring, following sewage diversion, the water was free of algal blooms, water clarity had greatly improved and M. heterophyllum began to inhabit the bay. By autumn of 1979, M. heterophyllum covered about 80% of the bay as a monospecific stand, the maximum depth of 4 m was visible, and total phosphorus concentrations of the water were generally below 20 mg P m^{-3} (Figure 28).

Sediment Sorption and Regeneration of Phosphorus

Sediments from Lees Mill were able to buffer phosphorus additions to waters, which had intimate contact with the sediments and restricted movement. Fifty ml wet hydrosoils covered with 200 ml distilled water or 200 ml of a 100 μg P l^{-1} solution did not differ significantly in their overlying water total phosphorus concentrations, after being incubated in vitro in the dark for 3 to 7 days. Phosphorus release of up to 24 μg phosphorus into the hypotonic, double distilled water from 50 ml of wet hydrosoils occurred. However, the 50 ml of hydrosoils sorbed up to 14 μg phosphorus from the phosphorus spiked distilled water (Table 10). Decomposition processes during the mud-water incubations did not lower dissolved oxygen levels below 1.6 mg l^{-1} or the pH below 5.4. Increased water movement over the sediments did not enhance the release of phosphorus from the hydrosoils into overlying waters, providing the sediments were not resuspended (Table 11).

Herbicide Induced Decay of Myriophyllum heterophyllum

Myriophyllum heterophyllum was actively rooted and growing in 6 aquaria for 52 days, prior to herbicide application with 2,4,5-TP and the water was clear. Ten days following herbicide application, plant die-back was observed. The M. heterophyllum was prostrate and mostly decayed 2 to 4 weeks after herbicide treatment, and 5 of the 6 aquaria had phytoplankton or periphyton blooms. Total phosphorus values ($\overline{X} \pm$ SE) were 23 $\pm$ 8 mg m^{-3} before application, 20 $\pm$ 6 mg m^{-3} ten days after herbicide treatment, and 27 $\pm$ 9 mg m^{-3}, 39 days after herbicide application. Though total phosphorus and algae levels increased following macrophyte decay, no other changes in water chemistry were noted. The dissolved oxygen levels never were below 5.2 mg l^{-1}, pH ranged from 6 - 7, and conductivity ranged from 39 - 60 μmho cm^{-1}, 25°C throughout the experiment.
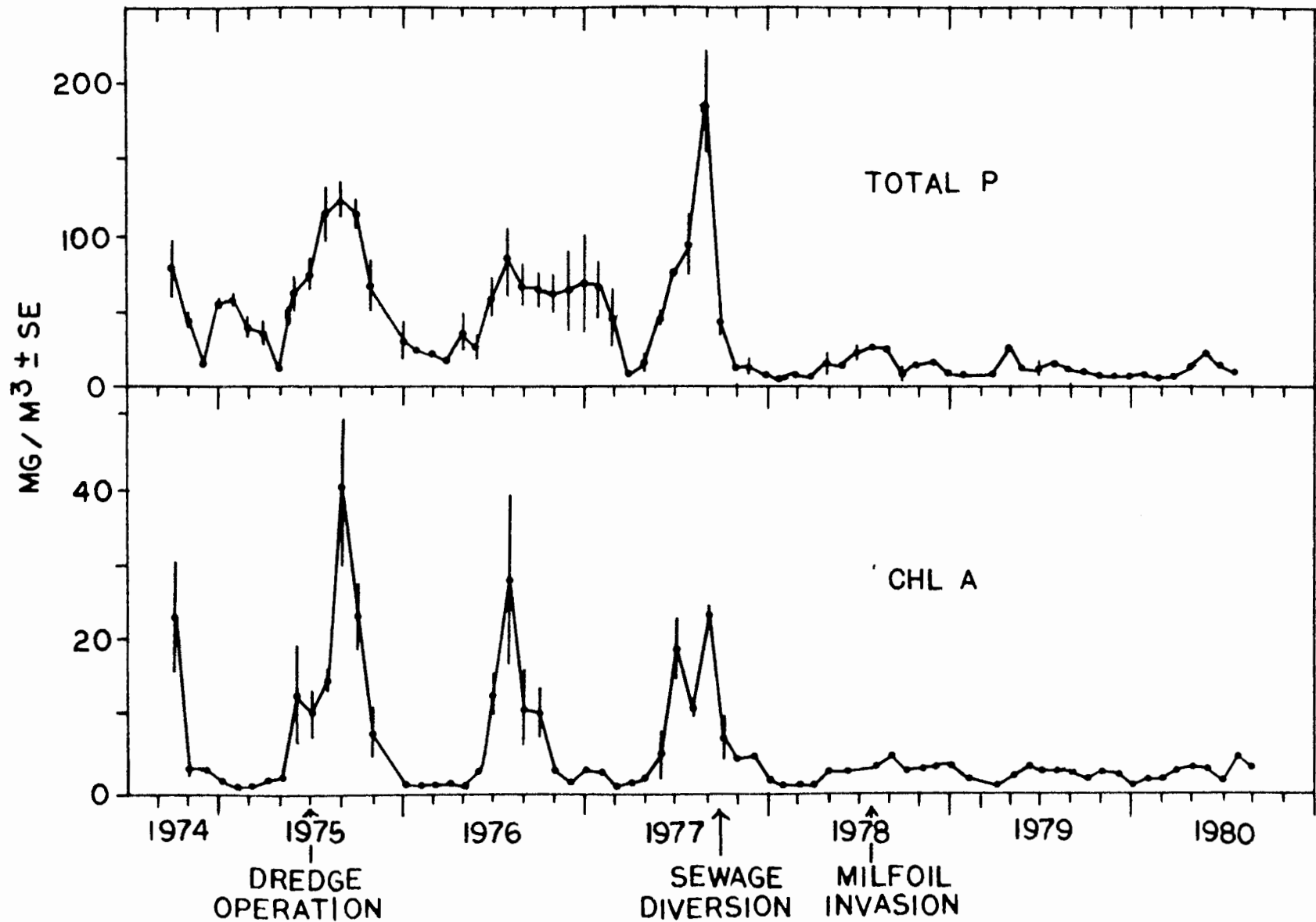
Figure 28. Total P and chlorophyll a levels in Front Bay, Lake Winnipesaukee (NHWSPCC)

TABLE 10. IN VITRO PHOSPHORUS ADDITION EXPERIMENTS
TO LITTORAL SEDIMENTS AND
OVERLYING DOUBLE DISTILLED WATER COLUMN
(Values are Total phosphorus (μg/l) in overlying water.)

Run 1. 7 day incubation using non-aerated double distilled water

Replicate	Mud + P	Mud	Distilled water + P	Distilled water
1	143	43	103	– –
2	36	47	98	– –
3	43	61	118	– –

Run 2. 3 day incubation using non-aerated double distilled water

Replicate	Mud + P	Mud	Distilled water + P	Distilled water
1	36	26	100	4
2	32	34	89	– –
3	60	40	111	– –

Run 3. 7 day incubation using aerated double distilled water

Replicate	Mud + P	Mud	Distilled water + P	Distilled water
1	106	96	98	– –
2	90	120	103	3
3	100	120	98	1

F values for TWO-WAY ANOVA for (Mud + P) versus (Mud) for all 3 runs

Test	df	F value
Mud + P vs Mud	1,12	0.28ns
Runs	2,12	9.95**
Interaction	2,12	0.74ns

TABLE 11. IN VITRO LITTORAL SEDIMENT AGITATION EXPERIMENT

Values are for total phosphorus (µg/l) in overlying water. Incubation period of 21 days with gentle agitation of 8 hours per day.

Replicate	Littoral lake water	Agitated littoral lake water	Littoral lake water + littoral mud	Agitated littoral lake water + littoral mud
1	7	10	28	27
2	7	8	16	19
3	7	7	16	18
4	7	7	18	18
5	13	10	23	16
$\overline{X} \pm SD$	8.2 ± 2.7	8.4 ± 1.5	20.2 ± 5.2	19.6 ± 4.3

ANOVA   df = 3,16   F value = 21.09**

Neuman - Keuls Multiple Range Test

Lake water (agitated)	Lake water	Mud (agitated)	Mud

Discussion

Since Hasler and Jones (1949) reported inhibition of phytoplankton by submersed hydrophytes, there has been much speculation whether this antagonism was nutritional, antibiotic or by physical shading. Brandl et al. (1970) observed a decrease in phytoplankton photosynthesis for phytoplankton incubated amongst submersed macrophytes. Philips et al. (1978) hypothesized that shallow waters receiving moderate nutrient loadings were dominated by macrophytes which suppressed phytoplankton through inhibitory secretions and competition for nutrients. Photosynthetic changes in water chemistry by submersed macrophytes, particularly increased pH and reduced CO_2 availability, are other possible inhibitory phenomena (Goulder 1969, 1970).

Contrary to Brandl et al. (1970), in situ incubations of phytoplankton at 0 and 1 m depths had greater chlorophyll a development amongst M. heterophyllum than in the open water. The submersed macrophytes possibly reduced the effects of destructive photo-oxidation processes by the high mid-summer light intensities in these surface waters, with the constantly shifting shade they provided the phytoplankton. Mid-day PAR levels in M. heterophyllum growths were similar to the open water, when shading was not present. The presence of macrophyte-released algicides inhibiting phytoplankton development is frequently cited, but has not been demonstrated. Myriophyllum heterophyllum and other submersed hydrophytes can strongly influence pH and CO_2 levels, which in return regulate algal species composition. Schindler et al. (1972), however, present evidence that the lower CO_2 concentrations during shifts to higher pHs does not limit phytoplankton standing crop.

Our enclosure experiments allowed for replication and manipulation of littoral conditions to test the importance of hydrosoils and the M. heterophyllum-periphyton complex in regulating phytoplankton growth. Major influences of isolation using enclosures included increased substrata for periphyton colonization, reduced turbulence and hence faster sedimentation, as well as stagnation of the water mass. Differences between control enclosures and natural conditions in the littoral waters were minor and temporal responses were synchronous. We conclude, similar to Landers (1979) and Twinch and Breen (1978a), that isolation of littoral waters does not exert a marked influence.

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The results of the enclosure experiments suggest that the added nutrient pulses were rapidly removed by either the muddy, organic sediments or the M. heterophyllum periphyton complex. Pulse nitrogen and phosphorus additions to enclosures with (a) littoral water and rooted M. heterophyllum, (b) littoral waters and sediments, and (c) littoral water, sediments and rooted M. heterophyllum did not significantly increase the phosphorus or chlorophyll a levels in the water. Furthermore, laboratory in vitro phosphorus additions to water with Lees Mill sediments were largely sorbed by the hydrosoils, consistent with the results of Fitzgerald (1970) and Harter (1968). Similarly, Lean et al. (1975) and Twinch and Breen (1978b) used enclosures and found low level pulse phosphorus fertilizations to isolated littoral waters with hydrosoils were quickly sorbed by the sediments, whereas repeated high level phosphorus enrichments stimulated algal blooms (Twinch and Breen 1981). Using experimental ponds, Ryan et al. (1972), Moss (1976), and Mulligan et al. (1976) also found that low level fertilizations to littoral waters, sediments and submersed macrophytes in experimental ponds caused little change in the phytoplankton. High nutrient additions produced extensive periphyton growth on submersed macrophytes, followed by phytoplankton blooms and the elimination of the submersed macrophytes. Although phosphorus "luxury uptake" by M. heterophyllum foliage occurs when phosphorus levels in the water increase (Chagnon and Baker 1979), detrimental growths of periphyton apparently are stimulated concurrently. Qualitative observations of M. heterophyllum receiving phosphorus fertilizations in our enclosures also revealed enhanced periphyton growth on these plants. Depression of submersed macrophyte production by dense epiphyte growth when nutrient levels in the water were increased has been reported by Cattaneo and Kalff (1980), Fitzgerald (1969), and Philips et al. (1978). The periphyton acts as a barrier for carbon uptake and reduces light intensity for the host macrophyte (Sand-Jensen 1977).

The phosphorus sorption ability of the hydrosoils will regenerate with cessation of phosphorus overloading. Following diversion of the phosphorus-rich sewage treatment plant effluent from Front Bay, total phosphorus and chlorphyll a levels rapidly declined and water clarity reached the bottom (Figure 28). Relieved of the phytoplankton's shading effect, M. heterophyllum colonized 80% of the Bay within 2 years, capitalizing on the rich store of nutrients in the sediments.

In summary, phytoplankton versus submersed macrophyte dominance in littoral waters is strongly regulated by the phosphorus characteristics of the hydrosoils. Low level phosphorus loadings are primarily sorbed by the sediments and support submersed hydrophyte growth. Phosphorus levels in the littoral waters increase when the littoral sediments' phosphorus sorption capacity, which is dependent on the type of hydrosoil and redox conditions, is exceeded by frequent, large dose pulses or continuous loading. When the waters' phosphorus levels exceed critical levels for a sufficient time to cause extensive periphyton growth, submersed macrophytes are stressed and eliminated. Phytoplankton dominance ensues, shading-out future submersed macrophyte growth. The sediments' phosphorus sorption ability will regenerate with cessation of phosphorus overloading, permitting submersed macrophytes to colonize littoral waters as phytoplankton dominance wanes.

Carpenter (1980) calculated that Myriophyllum spicatum can be a major source of phosphorus to lakewater during the summer, through the decay of fragmented tissue and not excretory leakage by the plant (Barko and Smart 1980). Decaying water milfoil fragments stranded amongst viable stems were omnipresent at my study sites and accounted for the $1 - 3$ mg m^{-3} higher phosphorus levels in the littoral compared to the limnetic waters. Phosphorus contributions to the water from herbicide-killed aquatic weeds can either be utilized in phytoplankton biomass production, or be sorbed by the sediments. Working with M. spicatum, Nichols and Keeney (1973) showed that water levels of phosphorus following herbicide treatment were greatly reduced by sediments. Similarly, herbicide treatment in three of my enclosures in 1978, resulted in rapid water milfoil decay and probably sediment sorption of the nutrients released. Herbicidal treatment of littoral waters having high plant biomass and stagnant water conditions will stimulate algal growth, because the sediments' phosphorus sorption ability will be overloaded. In the in vitro aquarium study, M. heterophyllum biomass was severalfold greater than natural conditions, the water was stagnant, and post-herbicide treatment algal blooms resulted.

Maximum algal growth in littoral waters supporting dense submersed hydrophyte communities commonly occurs in late summer or autumn (Kimball and Kimball 1977, Russo 1978, Wile and McCombie 1972). Such seasons correspond to the periods of emergent floral stem senescence and partial die-back of the submersed stems, respectively. Considerable decay and nutrient input result to stimulate phytoplankton increases (Landers 1979).

Our results are in agreement, as littoral water chlorophyll a maxima occurred in August - September 1977 and October - November 1978.

Summary

The competitive interactions for nutrients between submersed macrophytes, phytoplankton and sediments were examined, using in situ enclosures in the littoral zone of Lake Winnipesaukee, NH. The enclosure conditions were: M. heterophyllum naturally rooted in sediments, M. heterophyllum rooted through a polyethylene bottom to eliminate the sediment - water interface, sediments only and polyethylene bottomed enclosures without sediments or M. heterophyllum. Additions of nitrogen, phosphorus or nitrogen plus phosphorus were made weekly to biweekly to the enclosures, with the exception of controls. The enclosures and ambient conditions in M. heterophyllum stands were monitored for pH, dissolved oxygen, total phosphorus and chlorophyll a. Changes in the submersed macrophyte, total phosphorus and chlorophyll a levels were also monitored before and after cessation of continuous nutrient input from a sewage treatment plant into a shallow bay in Lake Winnipesaukee.

The results suggest that nutrient levels in the water determine whether submersed macrophytes or phytoplankton will dominate in the littoral zone. The littoral sediments' ability to sorb phosphorus loadings has a critical role in regulating phosphorus levels in the water. Phosphorus loadings as weekly pulses were removed from the water by the macrophyte-periphyton-sediment system. In contrast, continuous phosphorus loadings stimulated sufficient phytoplankton growth to inhibit macrophyte development. In M. heterophyllum stands, phytoplankton levels approximate oligotrophic conditions. Maximum phytoplankton levels normally occur during late summer or autumn, when part of the macrophytes' biomass decays during die-back. Herbicidal elimination of submersed macrophytes can stimulate phytoplankton growth, depending on environmental conditions. Macrophyte decay releases nutrients and requires oxygen. If the macrophyte decay releases nutrients in quantities sufficient to exceed the hydrosoils' sorption capacity, phytoplankton development may ensue. Dense macrophyte growths in stagnant water bodies are conditions most susceptible to secondary algal growths following herbicidal treatment of the macrophytes.

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APPENDICES

APPENDIX 1.   TWO-LEVEL NESTED ANOVA F VALUES FOR % DRY WEIGHT CONTENT OF 10 ELEMENTS AND ASH IN DIFFERENT TISSUES OF M. HETEROPHYLLUM COLLECTED FROM TWO SAMPLE SITES

Date	df	Ash	P	Na	K	Ca	Mg	Mn	Fe	Cu	Zn	Pb
13-VI-79	4,16	9.1**	40.5**	35.3**	1.7ns	5.7**	10.7**	7.0**	145.8**	2.4ns	0.4ns	4.3*
2-VII-79	5,20	14.6**	52.7**	52.5**	23.4**	79.5**	31.4**	11.8**	41.4**	1.1ns	13.4**	64.3**
25-VII-79	5,20	54.3**	34.4**	102.5**	44.2**	417.8**	48.6**	31.7**	86.8**	2.1ns	23.7**	112.2**
6-VIII-79	5,20	33.4**	16.6**	64.8**	32.3**	141.6**	100.3**	5.4**	15.0**	1.0ns	58.1**	1.0ns
26-IX-79	5,20	17.8**	14.7**	76.8**	17.7**	199.4**	0.5ns	14.0**	76.6**	8.0**	6.4**	7.5**
6-XI-79	4,16	12.2**	46.4**	103.7**	3.7*	27.4**	17.2**	15.9**	35.7**	0.3ns	2.0ns	22.3**
13-I-80	4,16	24.6**	64.5**	47.4**	35.2**	55.5**	15.7**	33.6**	65.8**	4.8**	10.4**	13.3**
3-III-80	4,16	26.7**	14.0**	19.7**	7.0**	29.0**	3.7*	20.4**	113.7**	5.6**	6.0**	16.6**
22-IV-80	4,16	9.6**	6.3**	22.2**	17.5**	19.9**	4.3*	12.8**	75.6**	4.3*	5.3*	15.1**
12-V-80	4,16	32.9**	45.9**	34.9**	30.3**	20.4**	19.1**	16.0**	32.8**	1.8ns	0.4ns	1.5ns
3-VI-80	4,16	25.2**	84.5**	111.1**	11.2**	25.5**	7.3**	58.8**	15.2**	2.4ns	1.3ns	24.2**
10-VI-80	4,16	45.6**	53.9**	50.0**	14.5**	71.3**	2.2ns	9.8**	16.6**	1.9ns	0.4ns	5.5**
30-VI-80	5,20	71.1**	35.8**	41.9**	19.0**	102.1**	3.3*	10.3**	41.2**	0.8ns	1.8ns	37.5**
21-VII-80	5,20	27.7**	25.1**	26.0**	39.6**	153.9**	35.1**	14.1**	33.9**	2.1ns	23.4**	36.3**

(ns = not significant)

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APPENDIX 2. TWO-LEVEL NESTED ANOVA F VALUES FOR % DRY WEIGHT CONTENT OF 10 ELEMENTS AND ASH FOR TISSUE - SITE INTERACTION OF M. HETEROPHYLLUM COLLECTED FROM TWO SAMPLE SITES

Date	df	Ash	P	Na	K	Ca	Mg	Mn	Fe	Cu	Zn	Pb
13-VI-79	4,16	2.72ns	0.64ns	0.46ns	0.79ns	1.99ns	0.32ns	2.06ns	0.81ns	1.14ns	1.15ns	0.45ns
2-VII-79	5,20	0.86ns	3.34*	1.58ns	0.21ns	2.57ns	0.68ns	1.48ns	1.38ns	1.11ns	0.17ns	0.64**
25-VII-79	5,20	1.00ns	5.05**	1.37ns	1.68ns	2.55ns	0.79ns	0.27ns	9.45**	0.81ns	3.07*	2.27ns
6-VIII-79	5,20	3.77*	3.14*	1.80ns	0.61ns	2.36ns	2.59ns	1.04ns	0.42ns	1.33ns	6.96**	0.94ns
26-IX-79	5,20	0.65ns	0.59ns	6.31**	1.39ns	2.20ns	2.97*	2.60ns	0.34ns	1.42ns	4.11**	0.11ns
6-XI-79	4,16	1.12ns	3.33*	11.30**	3.61*	1.34ns	2.84ns	2.29ns	0.72ns	0.18ns	4.15*	1.21ns
13-I-80	4,16	0.21ns	2.15ns	0.18ns	1.96ns	3.23*	2.61ns	0.68ns	0.35ns	0.39ns	2.88ns	1.09ns
3-III-80	4,16	4.59*	2.59ns	1.27ns	1.90ns	3.41*	1.29ns	0.89ns	2.58ns	0.37ns	1.02ns	0.53ns
22-IV-80	4,16	0.26ns	0.48ns	0.96ns	0.83ns	1.87ns	1.24ns	2.07ns	0.31ns	0.33ns	1.76ns	5.76**
12-V-80	4,16	0.95ns	1.69ns	2.04ns	4.47*	2.82ns	0.47ns	1.02ns	2.16ns	0.48ns	1.15ns	0.19ns
3-VI-80	4,16	1.28ns	0.25ns	1.18ns	0.15ns	0.90ns	0.05ns	0.03ns	0.52ns	0.99ns	0.85ns	0.37ns
10-VI-80	4,16	1.03ns	0.38ns	0.63ns	2.84ns	1.41ns	2.42ns	0.89ns	1.23ns	2.10ns	1.94ns	0.14ns
30-VI-80	5,20	2.07ns	0.57ns	1.18ns	0.97ns	1.35ns	0.37ns	0.35ns	0.58ns	1.26ns	0.60ns	1.45ns
21-VII-80	5,20	0.65ns	1.65ns	0.92ns	3.90*	0.79ns	0.56ns	2.89*	1.49ns	2.01ns	1.00ns	0.61ns

(ns = not significant)

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APPENDIX 3. F VALUES FOR ORTHOGONAL COMPARISONS OF % DRY WEIGHT TISSUE ELEMENT CONTENT IN M. HETEROPHYLLUM

(I = root vs. all other tissues, II = apex vs. subapex, III = root vs. stem immediately above the root, IV = apex vs. all other tissue, V = emergent flowering stem vs. all other tissues.)

Date	df	ASH I	II	III	IV	V	P I	II	III	IV	V
13-VI-79	1,16	0.6ns	0.9ns	0.1ns	7.7*	--	0.9ns	9.9**	4.3ns	40.3**	--
2-VII-79	1,20	4.2ns	0.4ns	1.1ns	1.2E38**	20.1**	2.2ns	4.0ns	5.8*	8.7**	54.9**
25-VII-79	1,20	48.7**	1.1ns	8.8**	15.4**	28.8**	5.0*	2E-3ns	2.9ns	14.4**	4.2ns
6-VIII-79	1,20	23.4**	3E-2ns	8.6E-1ns	13.7**	5.1*	0.7ns	0.9ns	4.5*	6.0*	7.2*
26-IX-79	1,20	6.3*	2.0ns	0.2*	10.1**	8.0*	0.4ns	4.1ns	2.1ns	17.7**	2.0ns
6-XI-79	1,16	2.3ns	1.3ns	0.3ns	10.2**	--	3.6ns	14.0**	1.1ns	51.0**	--
13-I-80	1,16	22.8**	2.4ns	12.2**	14.5**	--	1.6ns	16.9**	2.2ns	66.2**	--
3-III-80	1,16	28.2**	1.3ns	26.3**	5.9*	--	14.2**	0.8ns	3.3ns	0.5ns	--
22-IV-80	1,16	11.9**	0.4ns	5.2*	2.8ns	--	0.1ns	4.1ns	0.3ns	8.0*	--
12-V-80	1,16	31.3**	1.1ns	11.4**	17.0**	--	2.0ns	22.0**	1.2ns	55.8**	--
3-VI-80	1,16	17.5**	1.5ns	8.5*	15.5**	--	11.4**	16.6**	1.3ns	84.0**	--
10-VI-80	1,16	44.2**	2.9ns	15.1**	25.3**	--	7.3*	12.6**	2.0ns	53.5**	--
30-VI-80	1,20	46.8**	1.5ns	2.9ns	16.4**	51.1**	7.7*	1.4ns	1.3ns	14.0**	18.7**
21-VII-80	1,20	26.5**	0.1ns	3.8ns	7.0*	11.9**	4.5*	0.6ns	16.4**	12.2**	6.9*

(ns = not significant)

APPENDIX 3. cont.

Date	df	NA I	II	III	IV	V	K I	II	III	IV	V
13-VI-79	1,16	25.2**	0.001ns	3.84ns	15.2**	--	ns	ns	ns	ns	ns
2-VII-79	1,20	46.9**	0.05ns	34.8**	11.1**	23.4**	1.5ns	0.3ns	17.0**	1.1ns	9.9**
25-VII-79	1,20	51.7**	2.0ns	42.7**	1.8ns	70.2**	0.2ns	0.1ns	12.2**	2.9ns	33.7**
6-VIII-79	1,20	46.7**	0.6ns	30.3**	3.5ns	32.6**	1.2ns	0.01ns	9.6**	5.6*	15.9**
26-IX-79	1,20	39.1**	3.7ns	32.0**	0.6ns	52.2**	4.1ns	0.1ns	0.04ns	0.05ns	23.2**
6-XI-79	1,16	106.6**	5.1*	37.2**	0.01ns	--	2.35ns	0.3ns	1.6ns	0.005ns	--
13-I-80	1,16	28.3**	0.6ns	10.5**	1.9ns	--	3.9ns	0.5ns	4.8*	4.9*	--
3-III-80	1,16	14.9**	1.4ns	3.8ns	0.3ns	--	0.4ns	0.02ns	2.3ns	2.0ns	--
22-IV-80	1,16	16.9**	0.6ns	12.8**	1.7ns	--	0.1ns	6.4*	4.1ns	6.8*	--
12-V-80	1,16	34.1**	2.0ns	13.1*	19.2**	--	21.2**	9.4**	24.0**	15.9**	--
3-VI-80	1,16	96.5**	5.4*	16.1**	15.6**	--	14.2**	0.02ns	10.2**	1.6ns	--
10-VI-80	1,16	54.0**	2.0ns	15.0**	4.5ns	--	18.9**	0.1ns	13.3**	0.3ns	--
30-VI-80	1,20	30.1**	0.02ns	12.8**	16.7**	9.0**	0.3ns	0.1ns	7.0*	0.004ns	22.3**
21-VII-80	1,20	18.1**	0.002ns	10.1**	4.1ns	14.3**	1.2ns	0.6ns	33.0**	6.7*	1.7ns

(ns = not significant)

APPENDIX 3. cont.

Date	df	CA					MG				
		I	II	III	IV	V	I	II	III	IV	V
13-VI-79	1,16	5.5*	0.006ns	5.7*	0.02ns	--	6.9*	1.6ns	0.7ns	8.3*	--
2-VII-79	1,20	43.1**	0.02ns	19.6**	6.9*	97.0**	28.3**	0.005ns	6.8*	0.7ns	22.6**
25-VII-79	1,20	206.8**	0.01ns	47.0**	8.8**	595.9**	41.0**	1.2ns	2.6ns	11.8**	3.1ns
6-VIII-79	1,20	51.4**	0.2ns	6.9*	2.9ns	213.6**	84.4**	0.3ns	4.9*	36.9**	17.9**
26-IX-79	1,20	72.6**	0.7ns	4.9*	0.02*	288.9**	ns	ns	ns	ns	ns
6-XI-79	1,16	21.9**	0.9ns	6.1*	0.1ns	--	10.0**	0.1ns	0.1ns	4.0ns	--
13-I-80	1,16	36.0**	2.7ns	10.8**	2.3ns	--	19.5**	24.7**	14.8**	10.2**	--
3-III-80	1,16	21.9**	1.6ns	11.8**	2.1ns	--	2.5ns	0.04ns	0.3ns	0.2ns	--
22-IV-80	1,16	2.1E+6**	2E+7**	14.4**	3E+7**	--	4.8*	0.02ns	5.4*	0.1ns	--
12-V-80	1,16	25.5**	0.001ns	22.0**	1.4ns	--	10.8**	4.3ns	1.0ns	17.4**	--
3-VI-80	1,16	24.0**	3.9ns	23.9**	2.9ns	--	5.1*	2.4ns	2.0ns	6.9*	--
10-VI-80	1,16	0.01ns	553**	57.4**	18.1**	--	ns	ns	ns	ns	--
30-VI-80	1,20	73.4**	0.001ns	31.1**	1.5ns	127.5**	2.1ns	0.01ns	4.3ns	1.0ns	0.0004ns
21-VII-80	1,20	89.0**	0.01ns	12.6**	1.8ns	196.9**	17.6**	0.2ns	36.9**	0.07ns	0.8ns

(ns = not significant)

APPENDIX 3. cont.

Date	df	FE					MN				
		I	II	III	IV	V	I	II	III	IV	V
13-VI-79	1,16	187.8**	0.02ns	86.3**	20.8**	--	0.03ns	0.05ns	1.4ns	3.4ns	--
2-VII-79	1,20	68.6**	0.01ns	38.0**	2.9ns	4.6*	1.4ns	0.1ns	11.2**	1.7ns	3.1ns
25-VII-79	1,20	144**	0.01ns	81.5**	6.5*	7.5*	6.1*	1.0ns	33.0**	2.0ns	13.2**
6-VIII-79	1,20	24.9**	0.003ns	14.0**	1.0ns	1.6ns	1.1ns	4E-7ns	2.1ns	4.6*	0.3ns
26-IX-79	1,20	127.2**	0.04ns	69.4**	6.7*	6.8*	5.5*	10.4**	9.5**	7.5*	1.5ns
6-XI-79	1,16	40.8**	0.02ns	12.0**	7.0*	--	8.5*	7.3*	9.7**	7.3*	--
13-I-80	1,16	87.7**	0.05ns	56.6**	6.1*	--	19.5**	24.7**	14.8**	10.2**	--
3-III-80	1,16	150.8**	0.03ns	84.4**	12.9**	--	16.5**	14.5ns	7.3*	2.1ns	--
22-IV-80	1,16	100.6**	0.009ns	58.8**	7.3*	--	10.8**	4.0ns	12.3**	1.7ns	--
12-V-80	1,16	43.1**	0.01ns	22.7**	4.3ns	--	0.01ns	2.4ns	1.6ns	13.5**	--
3-VI-80	1,16	20.0**	7E-4ns	10.5**	1.8ns	--	5.0*	1.6ns	25.7**	26.7**	--
10-VI-80	1,16	22.1**	6E-4ns	12.3**	1.8ns	--	3.7ns	0.3ns	0.001ns	6.2*	--
30-VI-80	1,20	67.2**	0.01ns	31.6**	4.2ns	4.5*	0.08ns	0.09ns	6.5*	2.6ns	2.4ns
21-VII-80	1,20	55.0**	3E-4ns	24.8**	3.2ns	3.6ns	2.5ns	0.8ns	10.1**	4.8*	2.0ns

(ns = not significant)

APPENDIX 3. cont.

Date	df	ZN					PB				
		I	II	III	IV	V	I	II	III	IV	V
13-VI-79	1,16	ns	ns	ns	ns	--	5.2*	0.1ns	3.9ns	0.3ns	--
2-VII-79	1,20	4E-4ns	0.03ns	6.7*	3.5ns	3.1ns	107.1**	ns	4.6*	61.3**	4.6*
25-VII-79	1,20	15.5**	0.3ns	0.2ns	7.2*	10.4**	187.0**	ns	112.2**	7.5*	7.5*
6-VIII-79	1,20	25.5**	0.07ns	1.4ns	16.3**	16.3**	ns	ns	ns	ns	ns
26-IX-79	1,20	3.2ns	0.002ns	5.2*	0.02ns	1.1ns	12.5**	ns	7.5*	0.5ns	0.5ns
6-XI-79	1,16	ns	ns	ns	ns	ns	29.2**	ns	14.9**	3.0ns	--
13-I-80	1,16	0.5ns	9.1**	8E-4ns	13.6**	--	16.3**	0.5ns	7.6*	4.3ns	--
3-III-80	1,16	1.1ns	1.3ns	1.8ns	3.7ns	--	21.5**	ns	10.1**	2.0ns	--
22-IV-80	1,16	0.08ns	0.01ns	5E-4ns	2.2ns	--	19.7**	0.002ns	10.1**	2.2ns	--
12-V-80	1,16	ns	ns	ns	ns	--	ns	ns	ns	ns	--
3-VI-80	1,16	ns	ns	ns	ns	--	29.7**	ns	11.2**	4.1ns	--
10-VI-80	1,16	ns	ns	ns	ns	--	14.3**	ns	8.9**	0.9ns	--
30-VI-80	1,20	ns	ns	ns	ns	ns	59.8**	ns	24,9**	4.2ns	2.6ns
21-VII-80	1,20	25.0**	0.2ns	7.0*	5.7*	3.1ns	63.8**	ns	38.3**	2.6ns	2.6ns

(ns = not significant)

APPENDIX 4. PHOSPHORUS CALCULATIONS

A. Phosphorus Content of Harvestable Myriophyllum heterophyllum Stem Tissue

Parameter	Value	Data Source
Stem dry weight	0.01 g/cm	Lees Mill Cove, Lake Winnipesaukee
Stems/plant	10 stems/plant	Chagnon and Baker 1979
Plant density	17 plants/m^2	Chagnon and Baker 1979
Available height of stem for harvesting	150 cm	Aquamarine Corp.
Average stem phosphorus content	0.23% dry wt	Lees Mill Cove, Lake Winnipesaukee

Calculations for a 100 cm stem plant:

$$\frac{0.01 \text{ g dry wt}}{\text{cm stem}} \times \frac{100 \text{ cm}}{\text{stem}} \times \frac{10 \text{ stems}}{\text{plant}} \times \frac{17 \text{ plants}}{\text{m}^2} \times 0.23\% \text{ P dry wt} = 0.39 \text{ g P/m}^2$$

Calculations for a 150 cm stem plant:

$$\frac{0.01 \text{ g dry wt}}{\text{cm stem}} \times \frac{150 \text{ cm}}{\text{stem}} \times \frac{10 \text{ stems}}{\text{plant}} \times \frac{17 \text{ plants}}{\text{m}^2} \times 0.23\% \text{ P dry wt} = 0.59 \text{ g P/m}^2$$

B. Estimate of the Sediment Phosphorus Content (Data from Myriophyllum heterophyllum stands in Lake Winnipesaukee, Chagnon and Baker, 1979)

Average % P dry wt sediment:
Ostrands Marina = 0.025%
Greens Basin Beach = 0.040%
Alton Bay Beach = 0.072%

Assumption 1: M. heterophyllum rooting depth is 12 cm, so each m^2 of a milfoil stand is in contact with 0.12 m^3 of sediment.

Assumption 2: % dry wt content of sediment = 18% (Normandeau Assoc. 1977, data for sediment samples L01 A, L02 A, L06 B and L07 A in Lake Winnipesaukee)

Assumption 3: Sediment wet weight density = 1000 kg/m^3, therefore the kg dry weight per m^2 milfoil is:

$$\frac{0.12 \text{ m}^3 \text{ sediment}}{\text{m}^2} \times \frac{1000 \text{ kg wet wt}}{\text{m}^3 \text{ sediment}} \times \frac{18\% \text{ dry wt}}{\text{wet wt}} = 21.6 \text{ kg dry wt sediment/ m}^2 \text{ milfoil}$$

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Calculations of P content in sediments available to milfoil:

(1) Ostrands Marina = $\dfrac{21.6 \text{ kg dry wt sediment}}{\text{m}^2 \text{ milfoil}}$ X 0.025% P = 5.4 g P/m^2 milfoil

(2) Greens Basin = $\dfrac{21.6 \text{ kg dry wt sediment}}{\text{m}^2 \text{ milfoil}}$ X 0.040% P = 8.6 p P/m^2 milfoil

(3) Alton Bay Beach = $\dfrac{21.6 \text{ kg dry wt sediment}}{\text{m}^2 \text{ milfoil}}$ X 0.072% P = 15.5 g P/m^2 milfoil

C. Estimate of Phosphorus Removal from Sediments by Harvesting M. heterophyllum

1. Estimated Phosphorus content in the sediment available to milfoil ranges from 5.4 to 15.5 g P/m^2 milfoil (Appendix 4b).

2. Phosphorus content of harvestable M. heterophyllum stem (Appendix 4a):
   100 cm plant = 0.39 g P/m^2
   150 cm plant = 0.59 g P/m^2

3. Range of % Phosphorus removed from the sediments by one harvest of M. heterophyllum per year, assuming no P replenishment:
   100 cm plant = 2.5 - 7.2%
   150 cm plant = 3.8 - 10.9%

4. Range of % Phosphorus removed from the sediments by two harvests of M. heterophyllum per year, assuming no P replenishment:
   100 cm plant = 5.0 - 14.4%
   150 cm plant = 7.6 - 21.9%

5. Lake Winnipesaukee Phosphorus loading rate (Resource Planning Associates 1977)
   Moultonboro Bay, Lake Winnipesaukee: 0.30 g P/m$^2 \cdot$yr

6. Net loss of Phosphorus from the sediments per year, assuming two harvests per year, the first harvest of 150 cm plants and the second harvest of 100 cm plants:
   0.59 g P/m^2 + 0.39 g P/m^2 - 0.30 g P/m$^2 \cdot$yr = 0.68 g P/m$^2 \cdot$yr

7. Range of % Phosphorus removed from the sediments by two harvests per year (150 cm plants + 100 cm plants), assuming P loading rate of 0.30 g P/m$^2 \cdot$yr:
   4.4 - 12.6%

8. Number of years needed to deplete the Phosphorus pool in the sediments, assuming statement 7:
   7.9 - 22.8 years

APPENDIX 5a. F VALUES FOR 3-WAY ANOVA WITHOUT REPLICATES FOR JUNE 25,1979 LITTORAL PHYTOPLANKTON DATA
(includes 2 sites, 2 depths and 10 most numerous phytoplankton species)

	Depth	Site	Depth x site	Species	Depth x species	Site x species
df	1, 23	1, 23	1, 23	23, 23	23, 23	23, 23
F value	6.47*	0.71ns	2.77ns	2.28*	1.95ns	1.45ns

APPENDIX 5b. F VALUES FOR 3-WAY ANOVA FOR THE JULY 3 AND 21, 1980 PHYTOPLANKTON DATA FROM THE LITTORAL ZONE
(includes 2 depths with 3 replicates and 10 most numerous phytoplankton species)

	Depth	Species	Depth x species	Time	Depth x time	Species x time	Depth x species x time
df	1, 136	16, 136	16, 136	1, 136	1, 136	16, 136	16, 136
F value	0.20ns	15.10**	0.45ns	7.26**	6.12*	1.44ns	4.68**

APPENDIX 5c. F VALUES FOR 3-WAY ANOVA FOR THE JULY 3 AND 21, 1980 PHYTOPLANKTON DATA FROM THE LIMNETIC ZONE
(includes 2 depths with no replicates and 10 most numerous phytoplankton species)

	Depth	Species	Depth x species	Time	Depth x time	Species x time
df	1, 12	12, 12	12, 12	1, 12	1, 12	12, 12
F value	0.35ns	1.43ns	1.09ns	0.71ns	1.26ns	1.06ns

APPENDIX 6 a.   F VALUES FOR TWO-WAY ANOVA WITHOUT REPLICATES
FOR 1979 LITTORAL PLANKTON DATA

	SITE (2 littoral sites, 1 limnetic site)		SPECIES (10 most common phytoplankton species)	
Date	df	F value	df	F value
25-VI-79	2,34	2.99ns	17,34	3.08**
9-VII-79	2,34	2.31ns	17,34	4.49**
18-VII-79	2,34	2.74ns	17,34	.6.10**
25-VII-79	2,38	3.38*	19,38	4.59**
1-VIII-79	2,32	4.10*	16,32	6.57**
8-VIII-79	2,32	1.49ns	16,32	2.97**
15-VIII-79	2,28	1.90ns	14,28	5.48**

APPENDIX 6 b.   F VALUES FOR ORTHOGONAL COMPARISONS OF SITE DIFFERENCES

	LITTORAL VS LIMNETIC		LITTORAL SITE 1 VS LITTORAL SITE 2	
Date	df	F value	df	F value
25-VII-79	1,38	1920**	1,38	84.1**
1-VIII-79	1,32	408**	1,32	330**

APPENDIX 7. F VALUES FOR COMPLETELY RANDOM ANOVA FOR 1977 EXPERIMENTAL 0.8 m^2 CYLINDERS, 9 m^2 ENCLOSURE AND AMBIENT CONTROL

CHLOROPHYLL a ($\mu g/l$)

Sample date	Treatment prior to sampling	df	F value	Neuman - Keuls Multiple Range Test for Unequal Group Sizes[1,2]					
1-VIII	- -	5,8	0.87ns	P	NP	CM	C	E	A
10-VIII	Nutrient addition	5,8	18.00**	CM	P	C	NP	A	E
16-VIII	Nutrient addition	5,9	1.68ns	C	P	CM	NP	A	E
23-VIII	Nutrient addition	5,9	4.39*	C	P	CM	NP	A	E
6-IX	Nutrient addition	5,8	3.24ns	A	C	NP	CM	P	E
18-IX	Nutrient addition	5,9	4.33*	C	A	NP	P	CM	E
2-X	2x nutrient addition	5,8	4.17*	NP	C	P	CM	A	E
16-X	2x nutrient addition	5,8	3.82*	A	CM	C	NP	P	E
3-XI	2x nutrient addition	5,8	2.03ns	CM	P	C	NP	A	E
25-XI	2x nutrient addition	5,8	1.27ns	C	NP	P	A	CM	E

TOTAL PHOSPHORUS ($\mu g/l$)

29-VII	- -	5,8	1.41ns	P	NP	A	C	E	CM
3-VIII	- -	5,9	7.79**	A	C	NP	P	E	CM
10-VIII	Nutrient addition	5,9	7.93**	C	NP	P	CM	A	E
16-VIII	Nutrient addition	5,9	1.55ns	NP	C	P	CM	A	E
23-VIII	Nutrient addition	5,9	3.92*	C	CM	P	A	NP	E
6-IX	Nutrient addition	5,8	3.95**	NP	C	P	A	CM	E
18-IX	Nutrient addition	5,9	6.82**	P	A	NP	CM	C	E
2-X	2x nutrient addition	5,9	0.77ns	C	A	CM	P	NP	E
16-X	2x nutrient addition	5,9	2.27ns	A	C	E	P	CM	NP
3-XI	2x nutrient addition	5,9	13.80**	C	P	NP	CM	A	E
25-XI	2x nutrient addition	5,9	5.81**	NP	C	P	CM	A	E

[1] ranked from lowest to highest
[2] Zar 1974

A = ambient
C = control cylinders
CM = control cylinders with Myriophyllum heterophyllum
NP = cylinders with N + P additions
P = cylinders with P additions
E = enclosure with Myriophyllum heterophyllum and N + P additions

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APPENDIX 8. F VALUES FOR RANDOMIZED COMPLETE BLOCK DESIGN ANOVA FOR 1978 9 m^2 EXPERIMENTAL ENCLOSURES WITH M. HETEROPHYLLUM

CHLOROPHYLL a (µg/l)

Sample date	Treatment prior to sampling	df	F value	Neuman – Keuls Multiple Range Test[1,2]					
7-VII	- -	5,10	1.41ns	A	SC	NP	P	C	N
14-VII	Nutrient addition	5,10	1.55ns	NP	A	C	P	SC	N
20-VII	Nutrient addition	5,10	10.27**	A	N	C	NP	P	SC
13-VIII	Nutrient and Silvex addition	5,10	0.66ns	P	A	SC	C	N	NP
22-VIII	2x nutrient addition	5,10	1.63ns	A	NP	N	S	P	C
30-VIII	2x nutrient addition	5,10	2.07ns	S	A	C	N	NP	P
8-IX	2x nutrient addition	5,10	0.78ns	N	C	S	A	NP	P
16-IX	2x nutrient addition	5,10	1.34ns	A	P	S	C	N	NP
26-IX	2x nutrient addition	5,10	1.55ns	P	S	N	A	NP	C

TOTAL PHOSPHORUS (µg/l)

Sample date	Treatment prior to sampling	df	F value	Multiple Range Test					
7-VII	- -	5,10	4.6*	A	N	NP	P	SC	C
14-VII	Nutrient addition	5,10	2.9ns	A	NP	N	C	P	SC
20-VII	Nutrient addition	5,10	1.46ns	A	N	NP	C	P	SC
13-VIII	Nutrient and Silvex addition	5,10	0.66ns	P	A	SC	N	NP	C
22-VIII	2x nutrient addition	5,10	0.92ns	A	N	NP	P	C	S
30-VIII	2x nutrient addition	5,10	3.02ns	A	N	NP	C	S	P
8-IX	2x nutrient addition	5,10	0.51ns	N	NP	A	C	S	P
16-IX	2x nutrient addition	5,10	1.15ns	P	S	A	N	NP	C
26-IX	2x nutrient addition	5,10	1.72ns	S	N	P	A	NP	C

[1]ranked from lowest to highest
[2]Zar 1974

A = ambient
C = controls
SC = Silvex enclosures prior to herbicide application
S = enclosures after herbicide application
NP = enclosures with N + P additions
P = enclosures with P additions
N = enclosures with N additions

APPENDIX 9. F VALUES FOR COMPLETELY RANDOM ANOVA
FOR 1979 9m^2 ENCLOSURES

CHLOROPHYLL a (µg/l)

Sampling date	Treatment prior to sampling	df	F value	Newman-Keuls Multiple Range Test[1,2]		
25-VI	- -	2,6	0.69ns	C	NP	A
9-VII	Nutrient addition to NP	2,6	4.51ns	C	A	NP
18-VII	Nutrient addition to NP	2,6	3.96ns	C	A	NP
25-VII	Nutrient addition to NP	2,6	2.75ns	C	A	NP
8-VIII	Milfoil transplant to M-NP, nutrient addition to only M-NP	2,5	5.59*	M-NP	A	NP
15-VIII	Nutrient addition to only M-NP	2,5	8.64*	A	M-NP	NP
21-VIII	2x nutrient addition to only M-NP	2,5	6.64*	M-NP	A	NP
2-IX	2x nutrient addition to only M-NP	2,5	3.25ns	A	M-NP	NP
8-IX	Nutrient addition to only M-NP	2,5	2.88ns	M-NP	A	NP
18-IX	Nutrient addition to only M-NP	2,5	0.95ns	NP	A	M-NP

TOTAL PHOSPHORUS (µg/l)

Sampling date	Treatment prior to sampling	df	F value	Newman-Keuls Multiple Range Test[1,2]		
25-VI	- -	2,6	1.5ns	C	NP	A
9-VII	Nutrient addition to NP	2,6	7.91*	C	A	NP
18-VII	Nutrient addition to NP	2,6	39.51**	C	A	NP
25-VII	Nutrient addition to NP	2,6	7.46*	C	A	NP
8-VIII	Milfoil transplant to M-NP, nutrient addition to only M-NP	2,5	5.69*	M-NP	A	NP
15-VIII	Nutrient addition to only M-NP	2,5	5.07ns	M-NP	A	NP
21-VIII	2x nutrient addition to only M-NP	2,5	11.99*	M-NP	A	NP
2-IX	2x nutrient addition to only M-NP	2,5	5.76*	A	M-NP	NP
8-IX	Nutrient addition to only M-NP	2,5	0.65ns	A	NP	M-NP
18-IX	Nutrient addition to only M-NP	2,5	1.85ns	A	NP	M-NP

[1]ranked from lowest to highest   [2]Zar 1974

A = ambient
C = control enclosure without M. heterophyllum or sediments
NP = enclosure without M. heterophyllum or sediments but with N + P additions
M-NP = enclosure with M. heterophyllum, without sediments and with N + P additions