THE PHYSIOLOGICAL ECOLOGY OF EURASIAN WATERMILFOIL (*MYRIOPHYLLUM SPICATUM* L.) AND NATIVE MACROPHYTES IN LAKE GEORGE: DEPTH DISTRIBUTION OF BIOMASS AND PHOTOSYNTHESIS

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PREFACE

The authors gratefully acknowledge the support of this project by a Lake George Association Fund grant during 1987 and 1988. However, data and conclusions presented in this report are those of the authors alone.

Field and laboratory assistance for this project was provided by Valerie Alliger, Robert Cassady, Christopher Hartleb, Elizabeth Lawrence, and Leslie Taggett. Critical comments on this report were provided by Lawrence Eichler, Carolyn Madsen, and Reginald Soracco.

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EXECUTIVE SUMMARY

1. Light intensities are significantly reduced under a Eurasian Watermilfoil canopy, with light intensities reduced sufficiently to shade or restrict the growth of native plants, as well as induce self-shading of Eurasian Watermilfoil.

2. The biomass of M. spicatum is significantly higher than the two native species studied, P. amplifolius and P. praelongus. This is due to a higher density of growth, greater height, and the formation of a closed canopy.

3. Eurasian Watermilfoil allocates more leaf biomass to the upper canopy, with a steady reduction in stem biomass in the canopy with height. The pattern of leaf biomass allocation may be due to selection via self-shading, rather than created developmentally.

4. Myriophyllum spicatum has a higher maximum photosynthetic rate than the native species studied, but also has a higher light compensation point and light saturation point. Therefore, it requires a higher light-intensity environment. Thus, deeper depth zones are probably beyond the necessary light range of M. spicatum. Shallower depth zones with adequate light will allow M. spicatum to be more productive than native species, other environmental factors permitting.

CHAPTER 1

LITERATURE REVIEW AND HISTORY

This introductory chapter will provide the groundwork for the physiological ecology experiments performed during 1987-1988 by: 1) giving a detailed description of Lake George, its water quality and nutritional status; 2) describe the native plant community of the lake, and changes that have occurred since studies have been initiated; 3) review the invasion of Eurasian Watermilfoil into Lake George; and 4) review the ecology of the three species studied (Myriophyllum spicatum L., Potamogeton amplifolius Tuckerm., and Potamogeton praelongus Wulfen).

Lake George

Lake George is located in northeastern New York State, on the southeastern edge of the Adirondack Mountains and the Adirondack State Park in Warren, Washington and Essex Counties (Figure 1-1). The lake is divided into three distinct regions: the southern basin, the northern basin, and the Narrows which separates the two basins. Lake George is within the Lake Champlain drainage basin, with the lake's outlet at the north end. Pertinent morphological characteristics are presented in Table 1-1. Lake George is dimictic, with summer stratification present from June through October, and ice cover present from mid-January through March.

Lake George is an oligotrophic lake, with low alkalinity, low dissolved nutrients in the water column, and a high transparency (see Table 1.1). Nutrient levels in the shallow embayments tend to be greater than those in the open water, with total phosphorus ranging from 10-25 ugP l^{-1} and nitrate/ammonium ranging from 10-80 ugN l^{-1}. Although the overall lake trophic status is considered oligotrophic, signs of eutrophication have appeared, particularly in the southern basin. Transparency (as measured by Secchi Disk depth) has been declining in the southern basin, and is significantly less than transparency measured in the northern basin (Lawrence et al., 1989). More significantly, dissolved oxygen depressions in the southern-most deep basin of the lake, near Tea Island, have

been observed since 1982 (Eichler and Boylen, 1989).

Native Plant Communities

The native submersed aquatic plant communities were first intensively studied in 1973-1975, as reported in Sheldon and Boylen (1977) and Ogden et al. (1976). Ogden et al. (1976) report 42 submersed species in Lake George at that time. More recent studies, such as the 1987-1988 survey (RFWI et al., 1988; Madsen et al., 1989) and the 1987-1988 aquatic plant inventory (Taggett, 1989) have increased this list to 48 submersed aquatic vascular species.

The 1987 extensive survey of Lake George examined 43 sites along paired 100 meter transects at each location. As part of this survey, the presence of species at 2 m intervals along the transects was noted. The abundance of species and their rankings are given in Table 1-2.

The 1973-1975 survey was conducted by swim-overs of different sites, with the diver estimating the abundance of plants in each 1 meter depth interval. We have reinterpreted this data using only occurrence of the species at each site (Table 1-3). Comparing the most common species determined by this method of data analysis for the 1973-1975 survey with the results of the 1987 survey showed that the majority of the ten most common species found in each survey were the same (Table 1-4). Eight of the ten most common species were identical in the two surveys when the two charophytes (Nitella and Chara) from the 1987 survey are excluded. During the earlier survey, Eriocaulon septangulare was not observed as frequently as in 1987 due to a bias toward the south basin in the 1987 survey, and the tendency of this species to occur in waters less than 1 m depth (i.e., 0-1 m interval). Potamogeton pusillus was ranked 15 in 1987, the lower ranking possibly related to the senescence of the adult plants and formation of overwintering turions. Many of the Potamogeton species form their overwintering propagules and senesce by mid-summer, thus the 1987 survey may have been biased against these early-season plants.

In the 1987 survey, Juncus pelocarpus and Potamogeton foliosus were observed far more frequently than in the 1973-1975 survey, with P. foliosus not even cited by Sheldon and Boylen (1977). As both these species are quite small,

they may have been underestimated. The methodology used in the 1973-1975 survey may have caused small species to go unobserved.

Data expressed as a percent occurrence at sites studied versus the total number of sites studied presents a picture of which species were widely distributed in the lake, without implying how abundant those species may be at each site. Myriophyllum spicatum, which was not as widely distributed as most native species, ranked rather low (twenty-second), with 39% of sites having some Eurasian Watermilfoil evident in 1987. It was, however, generally more abundant at sites where it was found than many native plants, and therefore ranked higher (sixth) in overall frequency, as based on occurrence in all quadrats examined (RFWI et al., 1988).

In conclusion, the only significant difference in the vegetation of Lake George in the past 12 years is the introduction and spread of Eurasian Watermilfoil. It has gone from no representation in 1975 to one of the ten most abundant plant species in 1987, becoming widely distributed in the Lake George basin. Although no other major changes in native flora have been noticed as yet, further spread of Eurasian Watermilfoil could alter the current floristic composition, especially in reducing the abundance of species with a depth distribution to Eurasian Watermilfoil.

Invasion of Eurasian Watermilfoil

An exotic species from Europe and Asia, Myriophyllum spicatum (Eurasian Watermilfoil) was introduced to the Chesapeake Bay region of North America in the late 1800's (Reed, 1977). However, Eurasian Watermilfoil was first reported in nuisance proportions in the 1940's and 1950's. It soon began to spread across North America, and now has become established as a nuisance species as far west as British Columbia (Aiken et al., 1979).

Eurasian Watermilfoil was first noticed in Lake George in August of 1985, during sampling conducted by the Rensselaer Fresh Water Institute (RFWI) staff. Confirmation of the species by other authorities prompted further surveys of shallow embayments in Lake George. Two additional locations were discovered in 1985. Additional surveys were conducted by the Fresh Water Institute in 1986 to ascertain the extent of M. spicatum in the lake, resulting in twenty additional sites being located (RFWI, 1986). A cooperative research and monitoring program between the Fresh Water

Institute, New York State Department of Environmental Conservation (NYS DEC) and Adirondack Park Agency (APA) during 1987 and 1988 intensified the effort to locate and evaluate Eurasian Watermilfoil distribution in Lake George. In 1987, an additional 20 sites were located, raising the total known sites to 43 (RFWI et al., 1988). The continued efforts of 1988 found an additional 12 sites (Madsen et al., 1989). The current status of Eurasian Watermilfoil populations are discussed in annual survey reports, which is supported by the Lake George Association Fund.

Species Studied

Eurasian Watermilfoil (Myriophyllum spicatum L.)

Eurasian Watermilfoil was more typically thought to associated with eutrophic lakes of higher alkalinity, but it is now being recognized as more widespread than commonly thought. It generally overwinters as short green shoots or as a subterranean root crown, generally high in stored carbohydrates. Vegetative methods of spread are generally thought to be most significant, both for local growth of the clone as well as longer-distance dispersal via autofragments. Although the plant may flower and produce significant numbers of seeds (Madsen and Boylen, 1989), their importance to overall propagation is disputed (Aiken et al., 1979).

Hellquist and Crow (1983) placed the average alkalinity of lakes with M. spicatum at 60 mg $CaCO_3$ l^{-1}, significantly higher than the two other species studied. Myriophyllum spicatum thrives well at higher alkalinities due to its ability to use bicarbonate in photosynthesis (Grace and Wetzel, 1978). However, it can also survive in low alkalinity waters, where CO_2 predominates as the available form of dissolved inorganic carbon (Grace and Tilly, 1976).

Although four native species of Myriophyllum have been observed in Lake George, M. spicatum could only be confused with M. exalbescens. Myriophyllum exalbescens (or M. sibiricum Komarov; Aiken and McNeill, 1980) has rigid rather than flacid leaves and, although found sporadically around the lake, only had significant populations in Warner Bay (Madsen et al., 1989). Of the other species, M. verticillatum is similar in form to Eurasian Watermilfoil, but has much larger leaves and a characteristic apical meristem. Myriophyllum alterniflorum and M. tenellum are

common in Lake George, but are significantly different in appearance than Eurasian Watermilfoil.

In the Lake George Aquatic Plant Survey (RFWI et al., 1988; Madsen et al, 1989), Eurasian Watermilfoil was found throughout the 1 to 7 m depth range, but it was strongly biased towards the shallower depths, with a peak occurrence at the 3 to 4 m depth interval (Figure 1-2). This depth range coincides with that of several important native species, including Potamogeton amplifolius, P. praelongus, and P. zosteriformis. In addition, this is in the middle of the depth ranges of most submersed aquatic species and the depth of maximum macrophyte biomass in Lake George. Since Eurasian Watermilfoil is a recent invader, it was not observed in previous work (Ogden et al., 1976). In Lake George, dense bed communities have been found to a maximum of 4 meters depth, with scattered plants observed at deeper depths. In Saratoga Lake, dense beds also have been found to 4 meters depth, despite having a lower transparency than Lake George (Mikol, 1984).

The growth of beds and production of fragments is highly seasonal (Madsen et al., 1988). In many of the dense bed communities, percent cover and biomass data suggests that the Eurasian Watermilfoil is suppressing the abundance of native species and reducing species diversity. One mechanism for this may be shading by the dense overhead canopy (Madsen et al., 1989).

Large-leaf Pondweed (Potamogeton amplifolius Tuckerman)

This native plant is a common component of mesotrophic lakes, and generally grows as an open canopy of stems that can be up to 1 m tall, with many large, elliptical leaves. Hellquist and Crow (1980) place the average alkalinity of the distribution of this species at 32.6 mg $CaCO_3$ l^{-1}. Overwintering is by a rhizome, from which stems grow and by which the plant spreads. Flowering underwater is commonly observed, with seed formation also accomplished underwater. Little is known about its seed viability.

The depth range of P. amplifolius in Lake George (RFWI et al., 1988) was found to be from 1 to 6 m, with a decided peak of occurrence in the 2 to 3 m interval (Figure 1-2). Its depth range and relative importance make it a significant component in the shallow embayments in which Eurasian Watermilfoil may become abundant (Sheldon and Boylen, 1977; RFWI et al., 1988). Collins et al. (1987) indicated that it was most abundant in the south basin, and produces a significant proportion of the littoral

macrophyte biomass in the 2-4 meter depth range.

Whitestem Pondweed (Potamogeton praelongus Wulfen).

This species is also found in mesotrophic lakes, commonly at greater depths than P. amplifolius (Voss, 1972). This species tends to be the tallest of the Pondweeds. It has elongate, subcordate (somewhat heart-shaped) leaves that are sessile (e.g., no petiole), clasping the stem. Flowering may occur underwater, with successful seed formation possible on submersed flowers. Once more, little is known about seed viability or other aspects of sexual propagation. Potamogeton praelongus propagates from a rhizome, with new shoots being initiated after the senescence of mature flowering stems in late July. Hellquist and Crow (1980) place the mean alkalinity of waters containing this species at 47.2 mg $CaCO_3$ l^{-1}.

Potamogeton praelongus in Lake George was more abundant in the south basin than in the Narrows or north basin, contributing a significant fraction of littoral zone biomass in the 4-6 meter depth interval (Collins et al., 1987). Fine sediments appeared to favor its growth, as with P. amplifolius (Collins et al., 1987). Although found throughout the observed depth range of 1 to 7 meters in Lake George (RFWI et al., 1988), it was most common in the 3 to 6 meter interval (Figure 1-2). In these depths, it forms a sparse upper canopy under which is found a diverse bottom covering of other species, including P. amplifolius, P. robbinsii, and Vallisneria americana.

Potamogeton amplifolius and P. praelongus were selected in this study because they were abundant, have an upright growth form, and are tall for the genus Potamogeton in Lake George. It was hoped that they would be appropriate comparisons for M. spicatum.

Table 1-1. Morphometric and chemical characteristics for Lake George, New York.

Parameter	Units	Value	Reference
Morphometry			
Length	km	51	Swart & Bloomfield 1987
Shoreline	km	211	Swart & Bloomfield 1987
Mean Depth	m	18	Mikol & Polsinelli 1985
Max. Depth	m	58	Mikol & Polsinelli 1985
Surface Area	km^2	114	Mikol & Polsinelli 1985
Catchment Area	km^2	606	Mikol & Polsinelli 1985
Elevation	m	97	Mikol & Polsinelli 1985
Hydraulic Retention Time	yr	8.7	Mikol & Polsinelli 1985
Chemistry		**Average**	
Alkalinity	mg $CaCO_3$ l^{-1}	25	Eichler & Boylen 1989
pH	*	7.54	Eichler & Boylen 1989
Conductivity	umhos	96.8	Eichler & Boylen 1989
Total phosphorus	ug l^{-1}	5.3	Eichler & Boylen 1989
Chlorophyll *a*	ug l^{-1}	1.32	Eichler & Boylen 1989
Transparency (Secchi Disk)	m	9.2	Lawrence *et al.*, 1989

Table 1-2. Percent frequency and ranking of species based on number of sites at which it was found in Lake George during the 1987 extensive survey (data from RFWI et al., 1988).

Species	Number of Sites	Percent Frequency	Rank
Bidens beckii	18	44	19
Ceratophyllum demersum	4	10	32
Chara sp.	28	68	8
Elatine minima	16	39	21
Elodea canadensis	29	71	7
Eriocaulon septangulare	9	22	28
Fontinalis sp.	7	17	29
Heteranthera dubia	19	46	17
Isoetes echinospora	22	54	14
Isoetes macrospora	28	68	9
Juncus pelocarpus	26	63	10
Lobelia dortmanna	3	7	33
Myriophyllum alterniflorum	10	24	27
Myriophyllum exalbescens	1	2	38
Myriophyllum spicatum	16	39	22
Myriophyllum tenellum	19	46	18
Myriophyllum verticillatum	1	2	39
Najas flexilis	38	93	1
Najas guadalupensis	12	29	26
Nitella sp.	25	61	11
Potamogeton amplifolius	25	61	12
Potamogeton crispus	1	2	40
Potamogeton epihydrus	1	2	41
Potamogeton foliosus	30	73	6
Potamogeton gramineus	38	93	2
Potamogeton illinoensis	1	2	42
Potamogeton obtusifolius	3	7	34
Potamogeton pectinatus	3	7	35
Potamogeton perfoliatus	33	80	4
Potamogeton praelongus	14	34	24
Potamogeton pusillus	21	51	15
Potamogeton robbinsii	31	76	5
Potamogeton spirillus	23	56	13
Potamogeton zosteriformis	15	37	23
Ranunculus longirostris	20	49	16
Ranunculus reptans	14	34	25
Sagittaria cuneata	1	2	43
Sagittaria graminea	18	44	20
Sparganium angustifolium	3	7	36
Subularia aquatica	7	17	30
Utricularia minor	3	7	37
Utricularia vulgaris	5	12	31
Vallisneria americana	38	93	3

Table 1-3. Percent occurrence of macrophytes in Lake George study sites for 1973 through 1975 (from Sheldon and Boylen, 1977).

Species	Depth Range (m)	Number of Sites	Percent Frequency	Rank
Bidens beckii	2-7	18	36	12
Elatine minima	1	13	26	18
Elodea canadensis	1-7	22	44	10
Eriocaulon septangulare	1	31	62	7
Heteranthera dubia	1-3	18	36	13
Isoetes echinospora	1-5	18	36	14
Isoetes macrospora	5-7	32	64	6
Juncus pelocarpus	1-3	8	16	21
Lobelia dortmanna	1-2	6	12	24
Myriophyllum alterniflorum	1-3	12	24	19
Myriophyllum tenellum	1-2	18	36	15
Najas flexilis	1-5	41	82	2
Potamogeton amplifolius	2-5	28	56	9
Potamogeton crispus	1-3	3	6	25
Potamogeton gramineus	1-5	46	92	1
Potamogeton illinoensis	3	2	4	28
Potamogeton pectinatus	1	3	6	26
Potamogeton perfoliatus	1-5	31	62	8
Potamogeton praelongus	2-5	19	38	11
Potamogeton pusillus	1-5	39	78	5
Potamogeton robbinsii	2-7	40	80	4
Potamogeton spirillus	1	3	6	27
Potamogeton zosteriformis	2-5	7	14	23
Ranunculus longirostris	1-3	9	18	20
Sagittaria graminea	1-2	14	28	17
Subularia aquatica	1-2	8	16	22
Utricularia resupinata	1-2	16	32	16
Vallisneria americana	1-5	41	82	3

Table 1-4. Comparison of species ranking by site for the 1973-1975 and 1987 surveys (1973-1975 data from Sheldon and Boylen, 1977; 1987 Survey from RFWI *et al.*, 1988).

1973-1975 Survey Species	Rank	1987 Survey Species	Rank
		Chara sp.	8
		Juncus pelocarpus	10
Elodea canadensis	10	Elodea canadensis	7
Eriocaulon septangulare	7		
Isoetes macrospora	6	Isoetes macrospora	9
Najas flexilis	2	Najas flexilis	1
		Nitella sp.	11
Potamogeton amplifolius	9	Potamogeton amplifolius	12
		Potamogeton foliosus	6
Potamogeton gramineus	1	Potamogeton gramineus	2
Potamogeton perfoliatus	8	Potamogeton perfoliatus	4
Potamogeton pusillus	5		
Potamogeton robbinsii	4	Potamogeton robbinsii	5
Vallisneria americana	3	Vallisneria americana	3

Figure 1-1. The geographic location of Lake George in New York State (inset), and in relationship to Washington, Warren and Essex Counties.

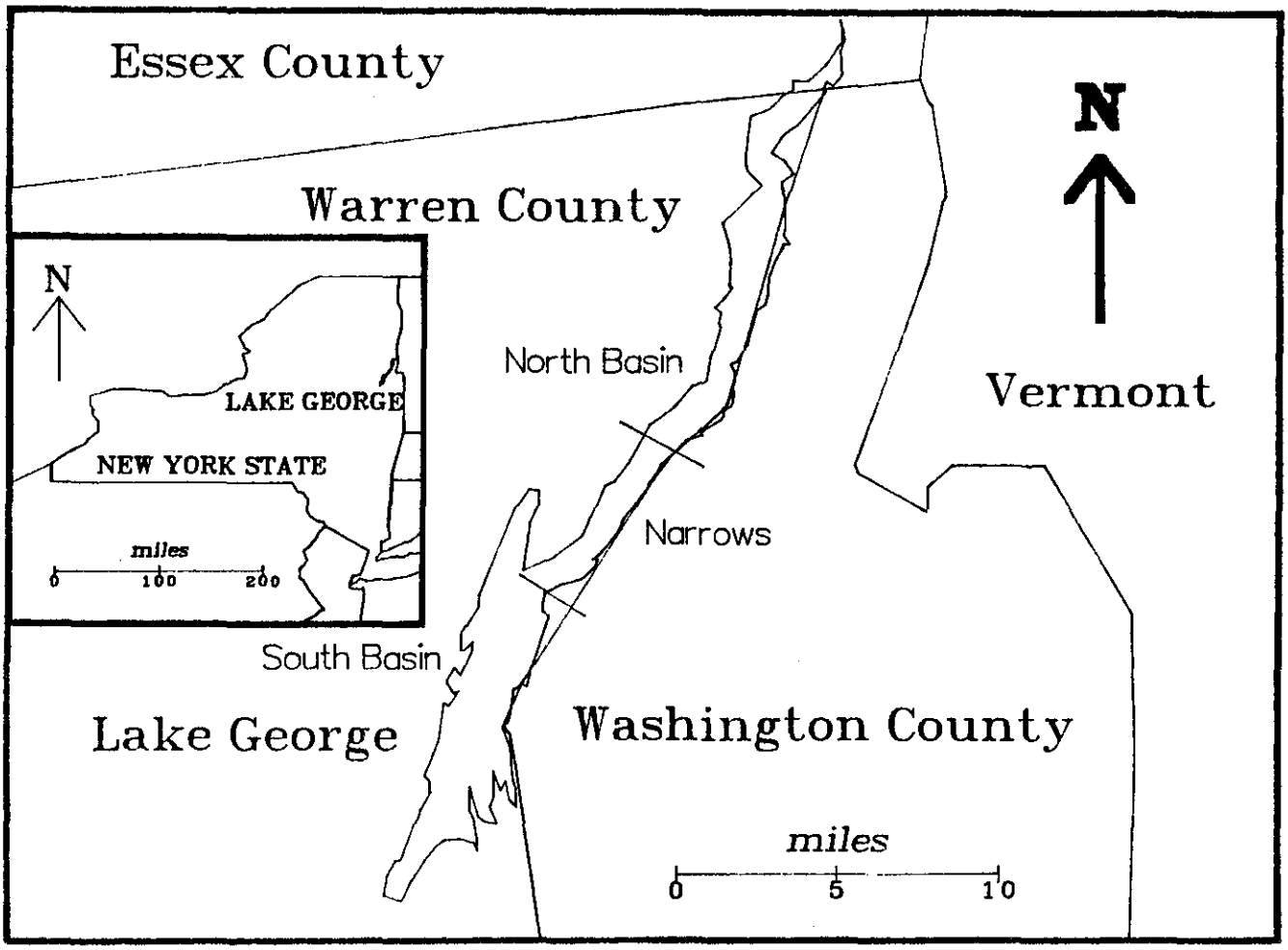
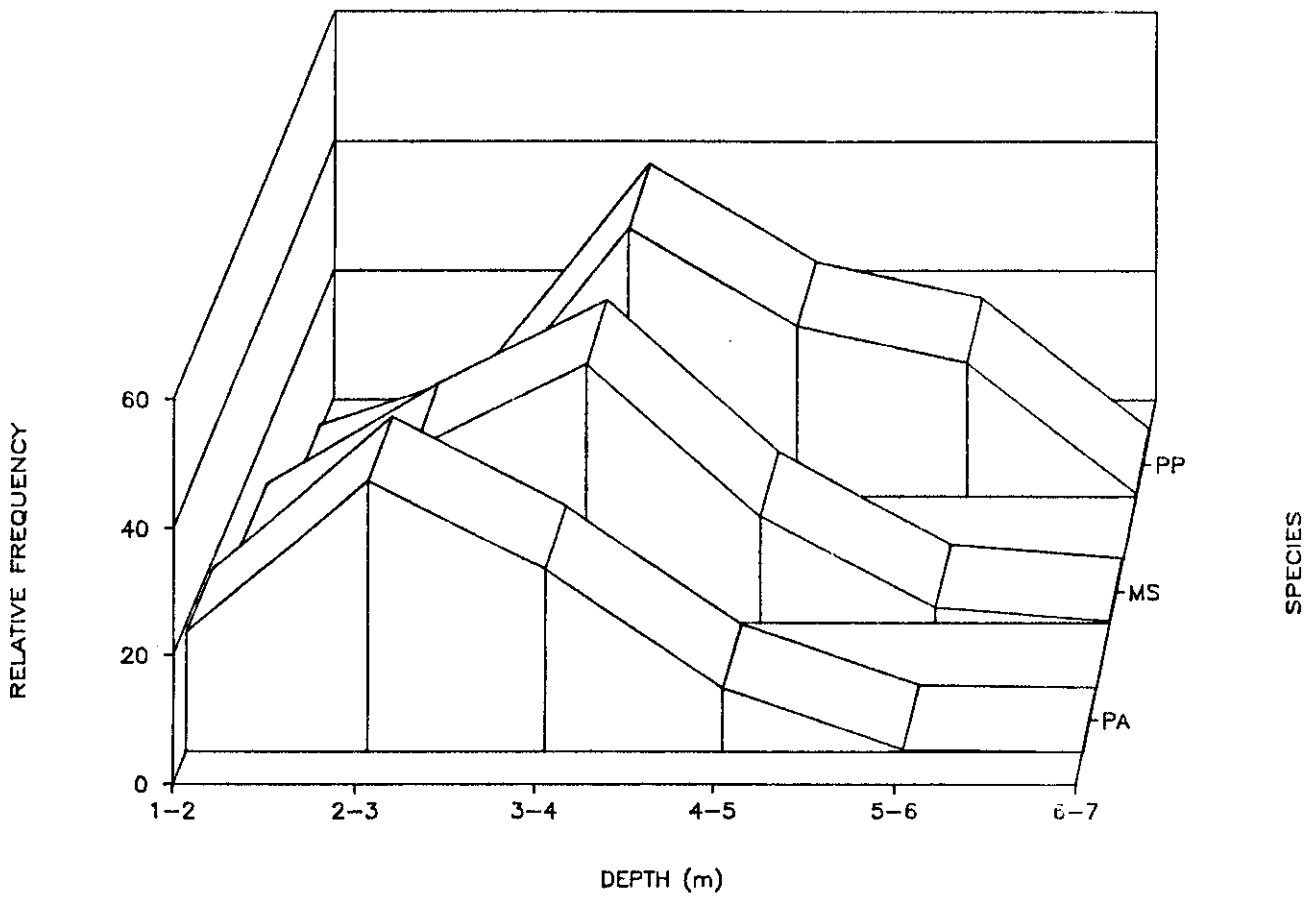


Figure 1-2. Depth distribution of Myriophyllum spicatum (MS), Potamogeton amplifolius (PA) and P. praelongus (PP) as indicated by relative frequency (data from RFWI et al., 1988).



CHAPTER 2

DEPTH DISTRIBUTION OF BIOMASS

Introduction

Eurasian Watermilfoil (Myriophyllum spicatum) has been characterized as having a densely branching surface canopy, created by having a caulescent (erect-stem) growth form with high stem density. Previous studies have indicated that it may possibly shade lower growing native plant species (Grace and Wetzel, 1978; Nichols and Shaw, 1986). Earlier studies by Titus and Adams (1979) have shown greater allocation to upper canopy biomass than the rosette-species Vallisneria americana. This allocation of biomass to the top of the canopy also accounts for increased photosynthetic ability on the whole plant level in situ (Adams et al., 1974).

This study was undertaken to document the biomass allocation with depth of leaves and stems for both M. spicatum and native species, comparing the relative form of the two canopies and strategies for displaying the photosynthetic units. Instead of choosing a rosette species, we chose two caulescent Potamogeton species, more similar in growth form to M. spicatum.

Materials and Methods

Study sites. The sites for sampling plant biomass are indicated in Figure 2-1. We sampled Huddle Bay and East Brook for all sample periods with the following exceptions: The first sample in 1987 was taken at Sunset Bay rather than East Brook, and the middle samples for the two Potamogeton species in 1988 were taken at Northwest Bay Brook rather than East Brook. Potamogeton amplifolius was absent from East Brook, so samples were only taken regularly from Huddle Bay, and P. amplifolius was only sampled during 1988. For more details on sites or species, see Chapter 1.

Methods. Light profiles were measured at each site for each sampling period (when possible) in open water areas and in the plant communities at 1 meter depth intervals using a Li-Cor 1000 Light meter and submersible quantum PAR probe, corrected using a quantum deck cell for incident

surface light. Light profiles were then expressed as the percent of light transmitted to depth compared to the light intensity near the surface. Light intensities beneath the plant canopies were also calculated as a percentage of the open water column readings for the same depth, thus giving a relative indication of the amount of shading occurring for each 1 meter depth interval.

Plant biomass was measured by collecting 6 randomly selected 0.1 m^2 samples from each community. For M. spicatum, this sample was simply dried at 70 C, and weighed. For the other species, the sample was divided into regular height intervals: 1 meter intervals for 1987, and 0.5 m intervals for 1988. Potamogeton amplifolius samples were divided into 0.25 m height intervals. In 1987, the number of stems and leaves for each interval was counted, then dried and weighed separately. During 1988, the samples were simply separated into stems, leaves and flowers, and then dried and weighed. For M. spicatum, ten randomly selected stems were collected in the field, and separated in the above manner for depth distribution percentages of stems, leaves and flowers. The entire biomass sample of M. spicatum was not used due to the extensive amount of sorting that would be required. Height of plant canopies was determined by measuring the maximum height of plant stems in each sample.

Results and Discussion

Light transmittance. As reported in the interim data report (Madsen and Boylen, 1988), light transmittance for 1987 sampling dates was significantly lower under the M. spicatum canopy than either the native plant canopy or open water profiles (Figure 2-2). This was also true during the 1988 sampling season, except for the sample period 1 June 1988 (Figure 2-3). In general, light profiles under native plant canopies were not different from open water profiles, indicative of the open canopy formation of the taller native plants. In contrast, dense beds of M. spicatum form a dense, closed canopy that effectively shades light. Light intensities under the M. spicatum canopy were consistently below 10% of surface light levels, a value which has been cited as limiting the growth of many native aquatic plant species (Madsen et al., 1989; Sheldon and Boylen, 1977).

The intensity of shading was more evident when the entire growing season at the two sites for both years was considered. In Figure 2-4, the light intensity of a given depth under the M. spicatum canopy is given as a percentage of the open water profile values for the same depth. At

both East Brook and Huddle Bay, the light intensities under the Eurasian Watermilfoil canopy are consistently between 5% to 50% of the open water light levels at the same depth. Similar graphs for P. praelongus show that the light profiles are typically similar to those of the open water, with the exception of near-bottom light levels (Figure 2-5). In many instances, dense macrophyte growths occur as a continuous canopy up to 0.1 to 0.5 meters above the bottom. Data for 1988 only indicates a similar relationship for P. amplifolius as was found for P. praelongus (Figure 2-6).

Height of plants. At both Huddle Bay and East Brook, in 1987 and 1988, M. spicatum was first measured to be 1 meter in height, with increasing height through late summer and early fall (Figure 2-7). Variation in height was small, indicating a synchronization in growth of stems, which would also contribute to an even, closed canopy. Canopy height reached a maximum of 1.8 to 2.2 meters for the sites measured, but greater heights have been observed. Water depth is indicated on these graphs to show the relationship between the top of the canopy and the surface of the water.

The height of P. praelongus exhibited a somewhat different pattern (Figure 2-8). The plants found in June were generally only 1 meter tall, or less, but grew rapidly in height to 2 meters by July and August. These plants typically flower and senesce by late August, as reflected in stem heights of less than a meter by September. Overwintering stems are generally less than 0.5 meters in height, as found in late October.

The height pattern observed for P. praelongus was also observed for P. amplifolius, but at a smaller scale (Figure 2-9). Maximum plant height was only 1 meter. Potamogeton amplifolius has a similar growth form, life history, and phenology to P. praelongus, which in part explains the similarity of these two species.

Biomass. The total shoot biomass for all three species at both sites for 1987 and 1988 is displayed in Figure 2-10. Myriophyllum spicatum shows a consistent pattern, with considerable variation between the two years studied. Peak biomass ranged from 125 to 250 g dw m^{-2} for 1987, to 350 to 600 g dw m^{-2} for 1988, at the two sites. Huddle Bay biomass was consistently lower than East Brook biomass. Our independent biomass estimates at Huddle Bay are nearly

identical to those obtained from biweekly sampling at Huddle Bay in 1988 (Madsen et al., 1989). Growth continued throughout the sampling season, with the exception of some dieback exhibited at East Brook in 1988.

Potamogeton praelongus biomass followed a similar pattern to that of this species' height, with a peak in biomass around late June or early July. This pattern was also apparent for P. amplifolius. Biomass for P. praelongus was not different between East Brook and Huddle Bay.

Biomass Allocation. Biomass allocation between stems and leaves was fairly consistent for M. spicatum, with 40%-50% of biomass allocated to leaves, the remainder allocated to stems (Figure 2-11). The relatively high amount of stem material may in part be due to high turnover of leaves, and leaf sloughing during the growing season. Allocation patterns for P. praelongus (Figure 2-12) shows that a higher proportion, 50%-60%, of biomass is allocated to leaves. Less than 5% of biomass was allocated to flowering structures during flowering in July. Since P. praelongus does not branch, relatively less material needs to be used for stems. Potamogeton amplifolius is similar to P. praelongus, with 60% or more of biomass found in leaves (Figure 2-13).

The lower percentage of leaf biomass in M. spicatum may be explained in part through two factors. First, M. spicatum has small leaves versus the large leaves of the Potamogeton species studied, and M. spicatum has more branching to accomodate and effectively display these smaller leaves. Secondly, the high rates of leaf senescence and sloughing reduces the standing leaf biomass at a given time, but total leaf production may actually be more comparable to the Potamogeton species.

Less than 2% of biomass was allocated to flowering during the July sampling. Since these three species predominantly propagate vegetatively, the low allocation to flowering was not unexpected. Vegetative propagation justifies more resources into stem and leaf material. Further studies into allocation of plant material to other structures, such as vegetative propagules, roots, and rhizomes would be beneficial.

Depth Distribution of Biomass. Biomass depth distribution data for 1988 samples of M. spicatum, as shown in Figure 2-14, were divided into 0.5 meter height intervals from the

bottom to the top. June samples indicated a largely basal growth of short stems, a typical overwintering form. Results for August and October were quite similar, with leaf biomass showing a pronounced peak near the top (2 meters), with few leaves shown at the 0.5 or 1 meter interval. The absence of leaves here was the result of sloughing caused by canopy self-shading. Stem biomass was more evenly divided between the depth strata, with greater biomass at the base for support, and decreased biomass as stem height increased. This was consistent with stem allometry for other plant species.

Biomass depth distribution in 1988 for P. praelongus was quite distinct (Figure 2-15). Distributions for June and October represented largely short plants. The profile for July represented full-grown plants. In this profile, distribution patterns between stems and leaves were almost identical, with the exception of slightly decreased basal biomass of leaves, and increased biomass of stems. This pattern was distinct from that of M. spicatum, which exhibited substantially more biomass to leaves near the surface. Since the pattern observed for M. spicatum was the result of leaf senescence due to self shading, one would not expect a similar pattern for the open-canopy growth of P. praelongus.

Potamogeton amplifolius biomass distribution showed a strong tendency for biomass allocated near the base of the plant, where it tended to form a somewhat denser canopy, with interspersed taller shoots (Figure 2-16).

Conclusions

As in 1987, field measurements in 1988 indicated that the canopy formed by dense growths of M. spicatum greatly reduced light transmittance, as compared to native plant canopies and open water profiles. Light level reductions could be sufficient to shade native species, as well as causing self-shading of M. spicatum leaves in the lower portions of the canopy.

Myriophyllum spicatum canopy heights typically reached a maximum of 2 to 2.4 meters, by late August or September. Potamogeton praelongus was of similar height, with P. amplifolius significantly shorter, at a little over 1 meter.

Total biomass of M. spicatum continued to increase

throughout the measured season, with maximum values of up to 600 g dw m^{-2}. Potamogeton amplifolius and P. praelongus had maximum biomass levels in early July, with rapid biomass decrease afterwards. Maximum biomass was 100 g dw m^{-2} and 125 g dw m^{-2}, respectively. Biomass allocation between stems and leaves differed. Myriophyllum spicatum allocated only 40% to 50% of biomass to leaves, whereas P. amplifolius and P. praelongus allocated from 50% to 70% of biomass to leaves. However, leaf turnover is probably higher in M. spicatum.

Biomass depth distribution profiles for M. spicatum from 1988 clearly show a strong trend in leaf biomass allocation towards the surface, with stem allocation decreasing from bottom to top. In contrast, P. amplifolius and P. praelongus biomass clearly decreases from bottom to top for both stems and leaves. However, the top-heavy allocation of leaf biomass in M. spicatum is undoubtedly due to the senscence of leaves from self-shading rather than a developmental pattern, resulting in leaf turnover and loss, which is an excessive expenditure of plant resources.

Figure 2-1. Sample sites for depth distribution of biomass studies in Lake George, New York with an inset indicating the location of Lake George in New York.

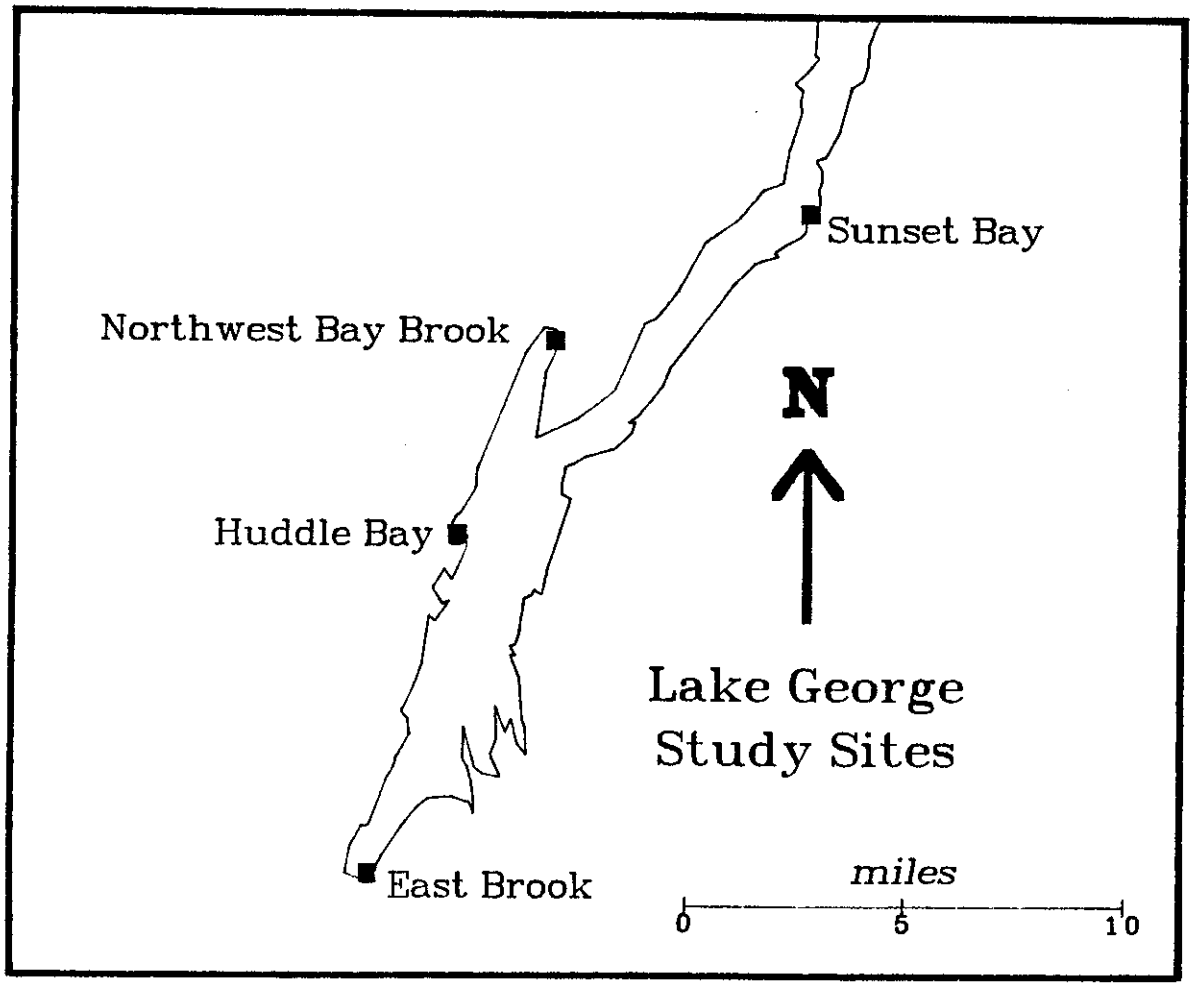


Figure 2-2. Percent light transmission profiles for Huddle Bay and East Brook in the open water, native community, and milfoil community sites during 1987.

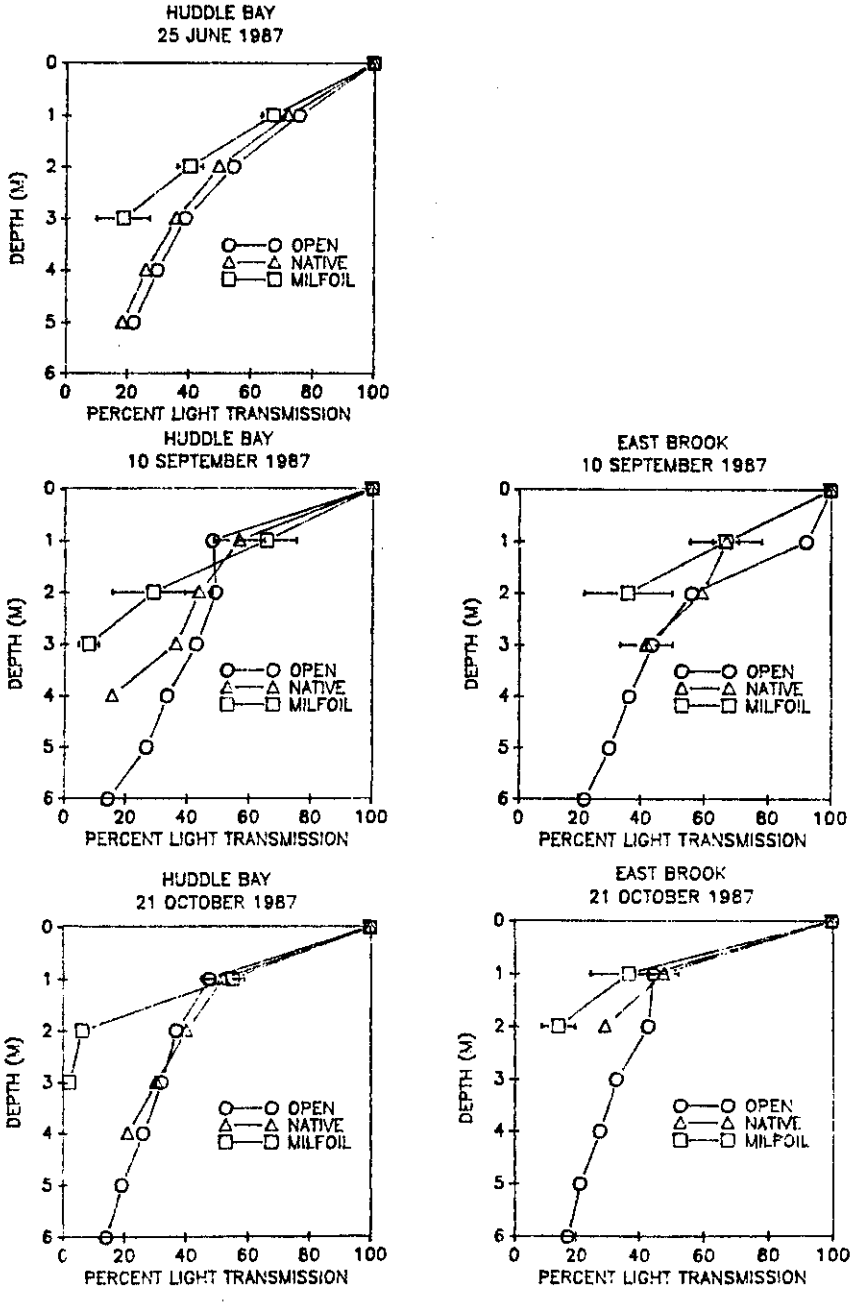


Figure 2-3. Percent light transmission profiles for Huddle Bay and East Brook in the open water, P. praelongus (PP) community, P. amplifolius (PA) community, and milfoil community sites during 1988.

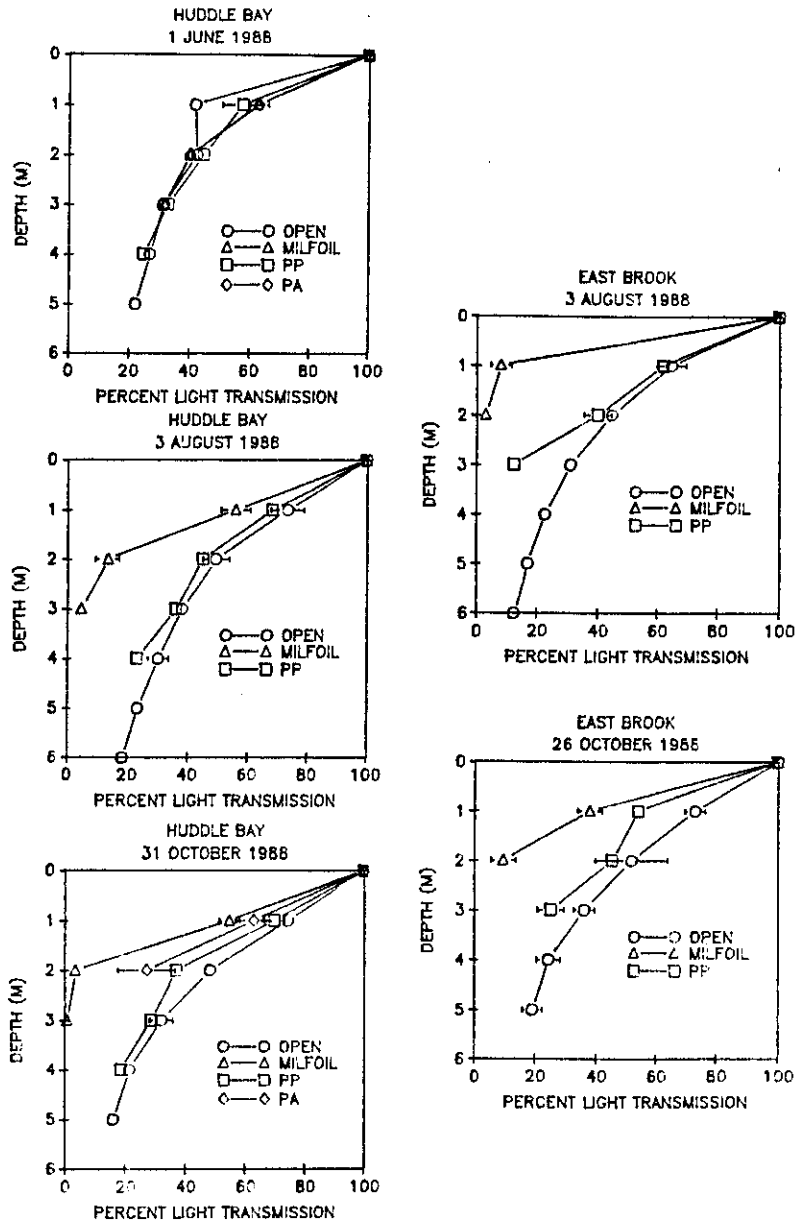


Figure 2-4. Percent of open water column light penetration for a given depth within the M. spicatum community during 1987 and 1988.

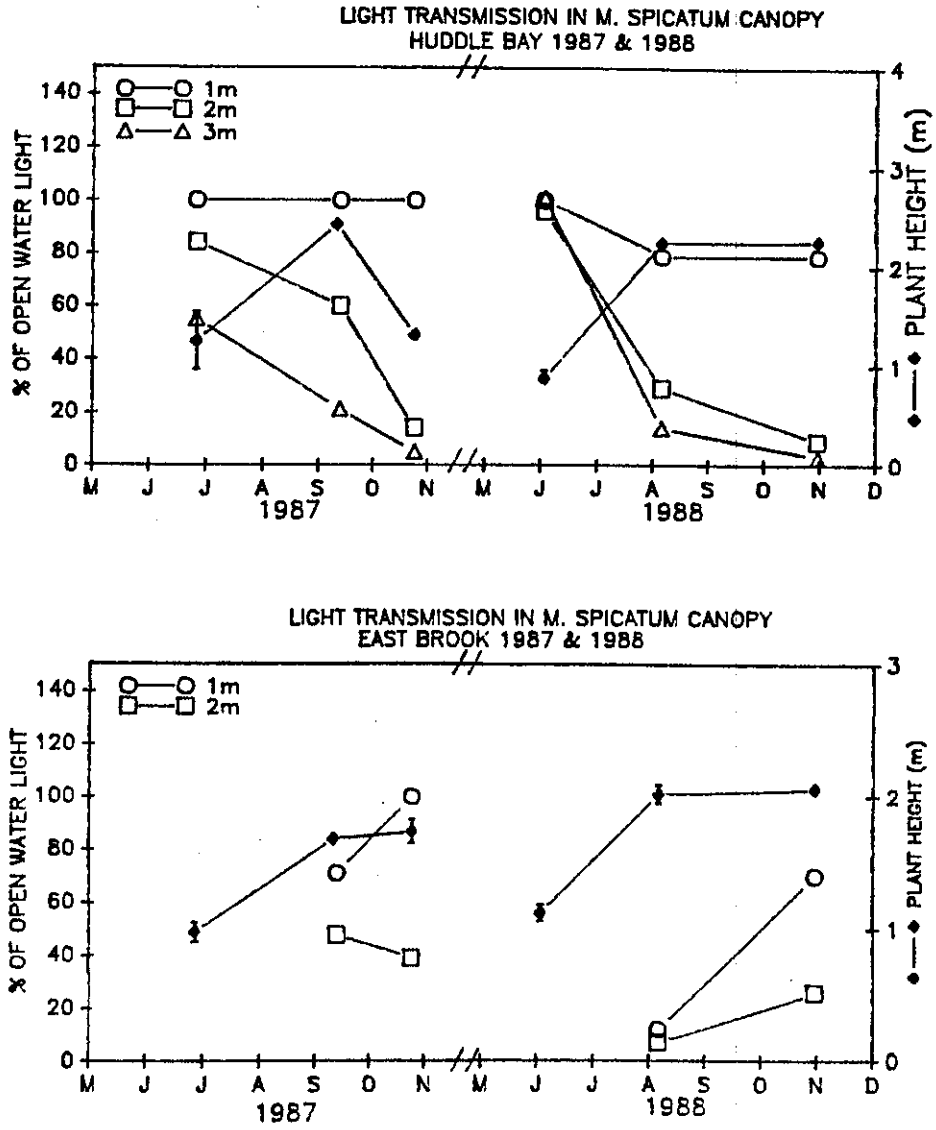


Figure 2-5. Percent of open water column light penetration for a given depth within the P. praelongus community during 1987 and 1988.

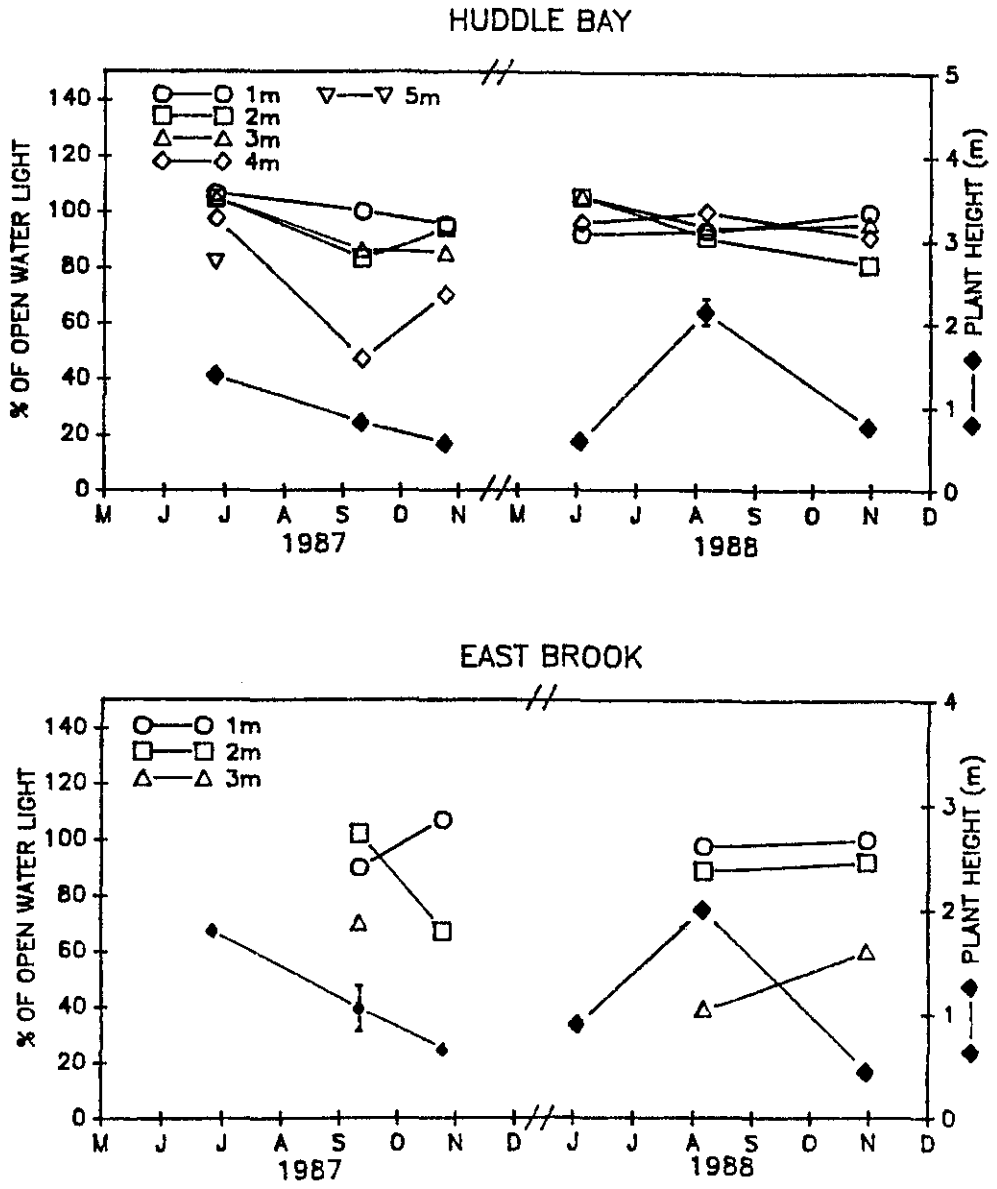


Figure 2-6. Percent of open water column light penetration for a given depth within the P. amplifolius community during 1988.

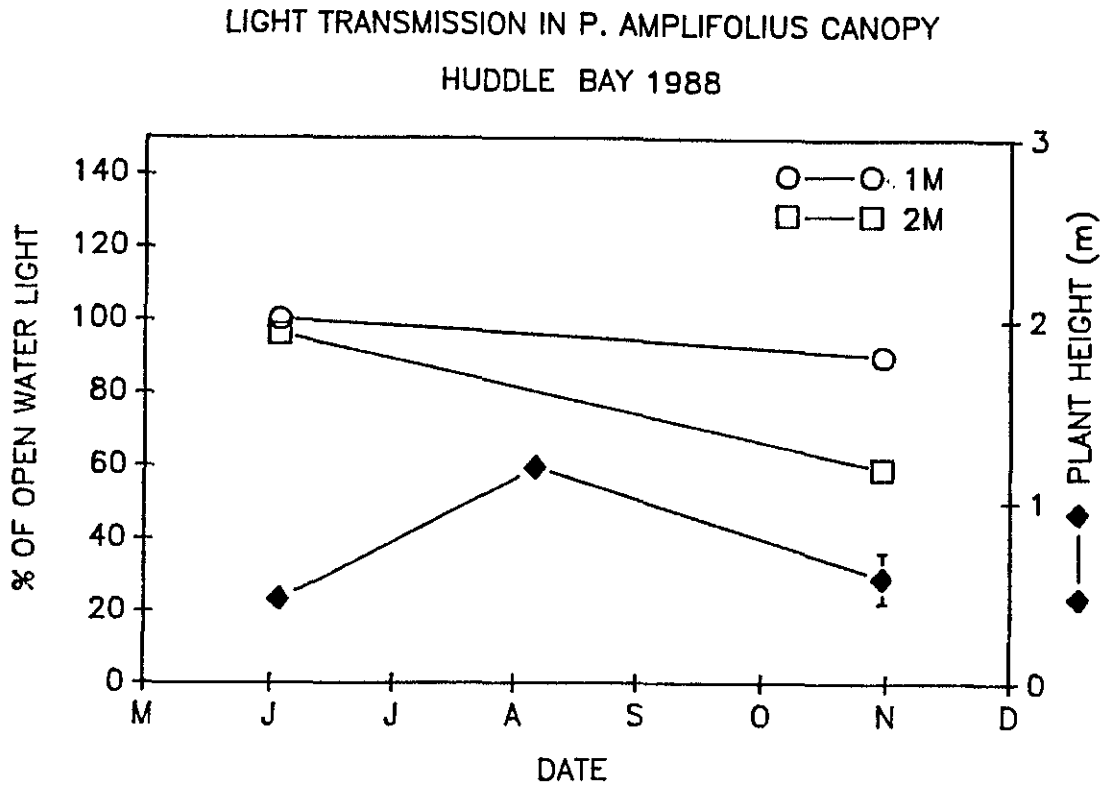


Figure 2-7. Height of Eurasian Watermilfoil at Huddle Bay and East Brook during 1987 and 1988.

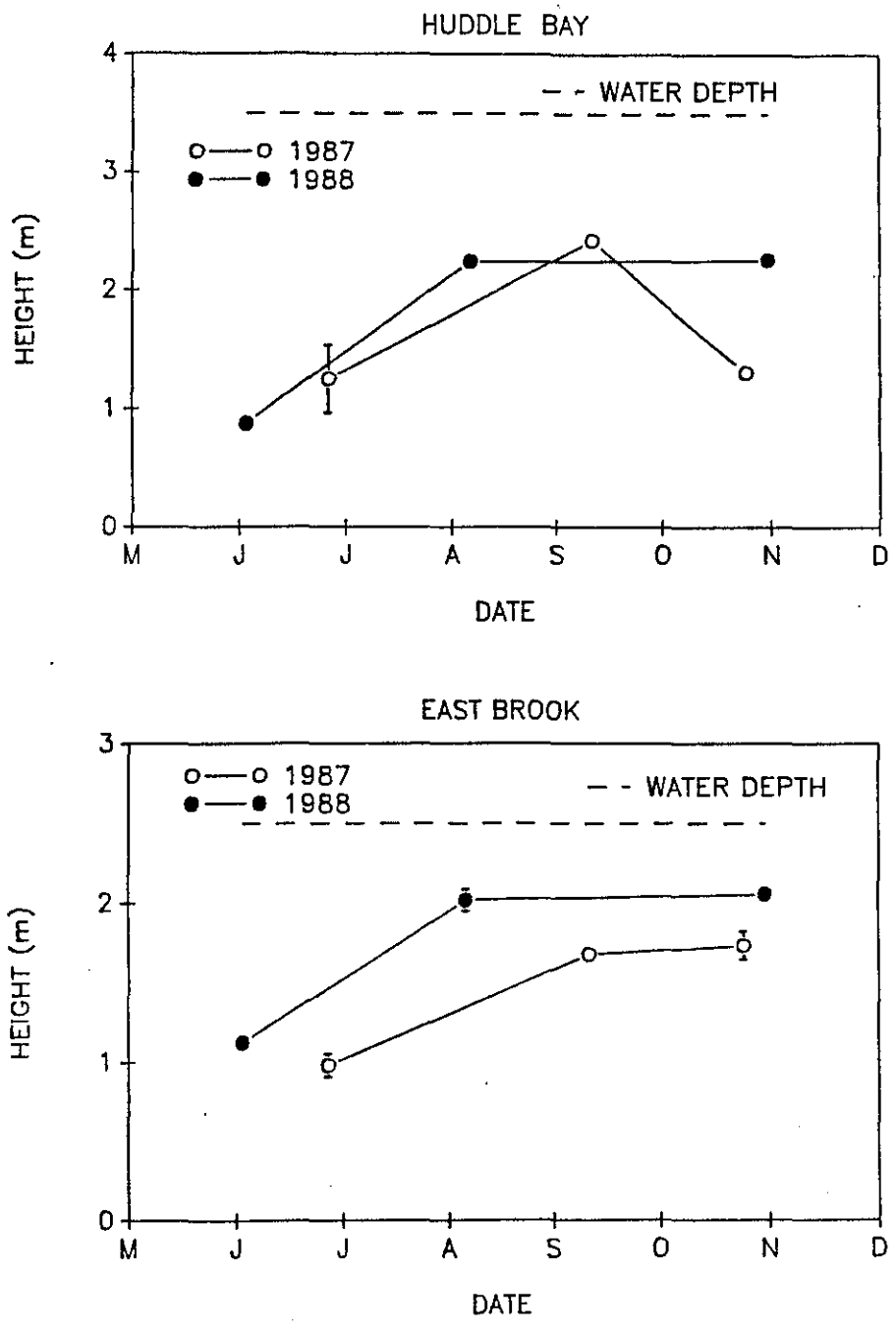
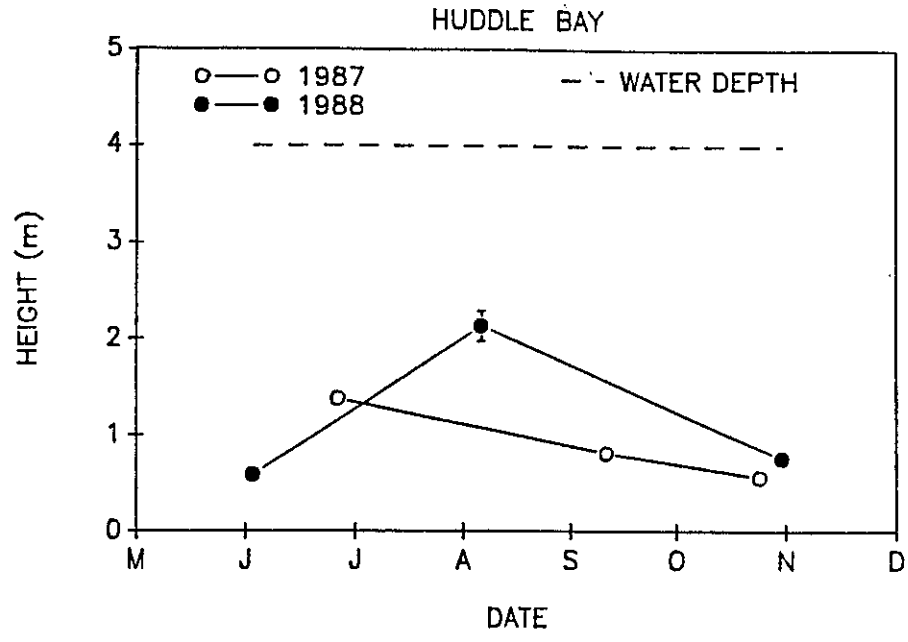


Figure 2-8. Height of P. praelongus at Huddle Bay and East Brook during 1987 and 1988.



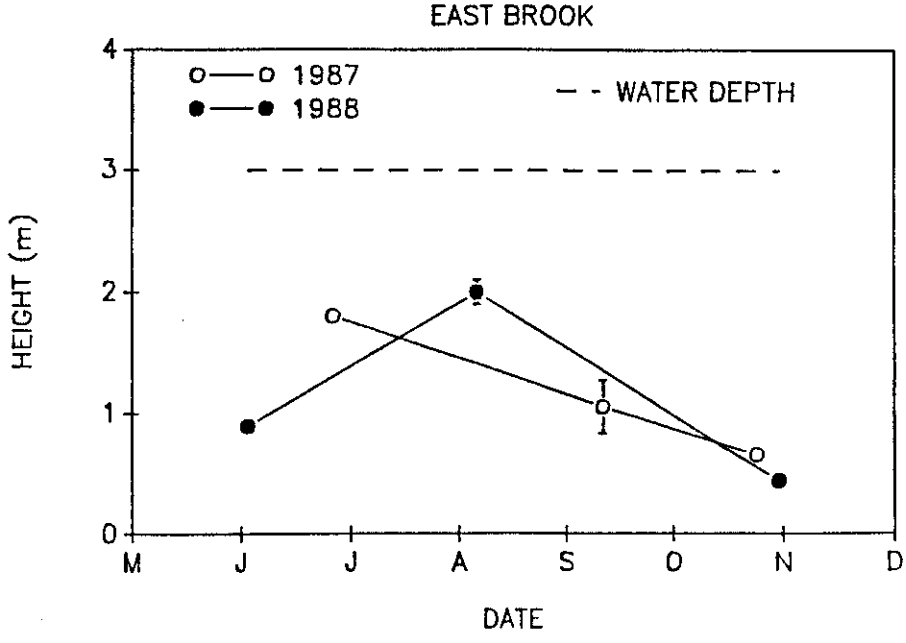


Figure 2-9. Height of P. amplifolius at Huddle Bay and Northwest Bay Brook during 1988.

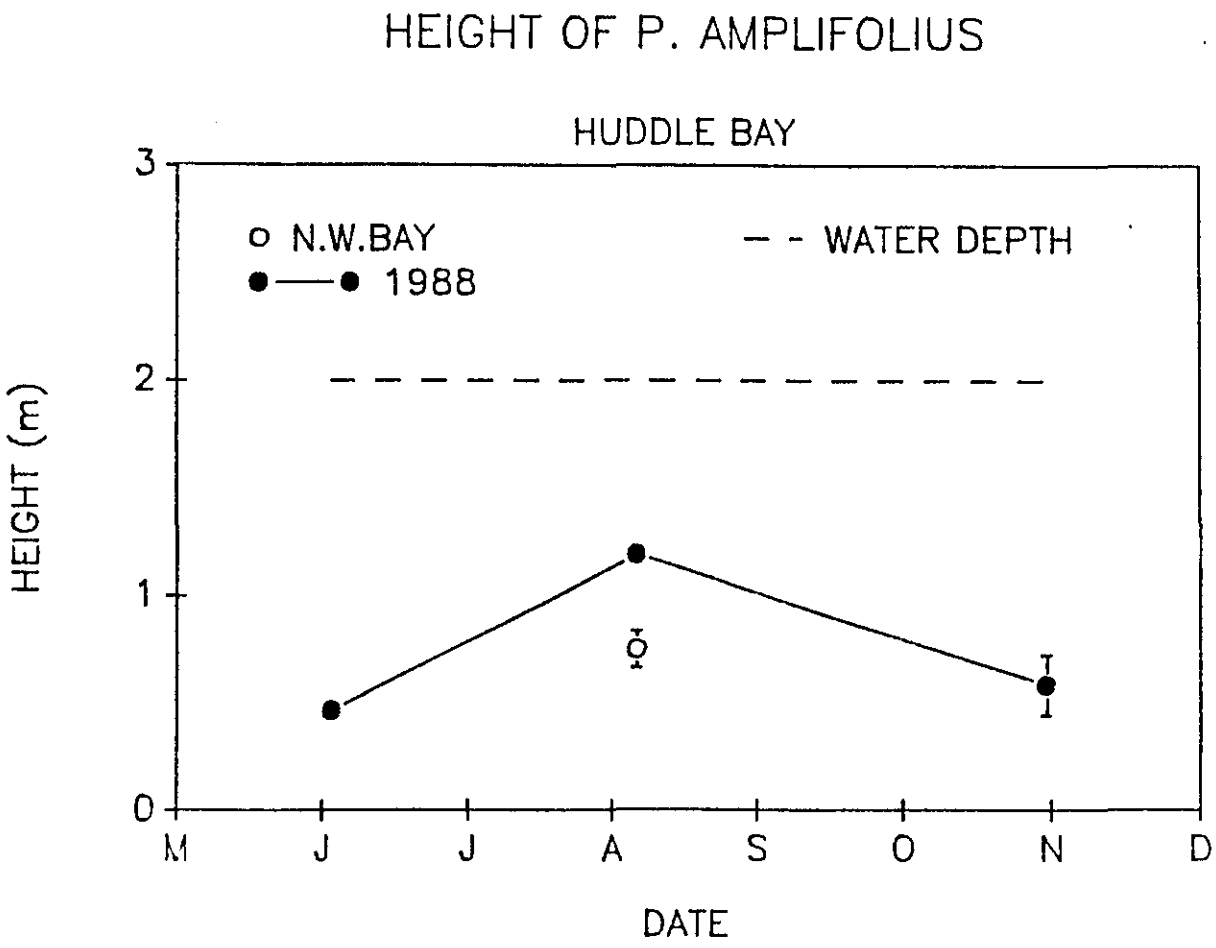


Figure 2-10. Total biomass of M. spicatum, P. praelongus and P. amplifolius during 1987 and 1988 at Huddle Bay, East Brook, and Northwest Bay Brook.

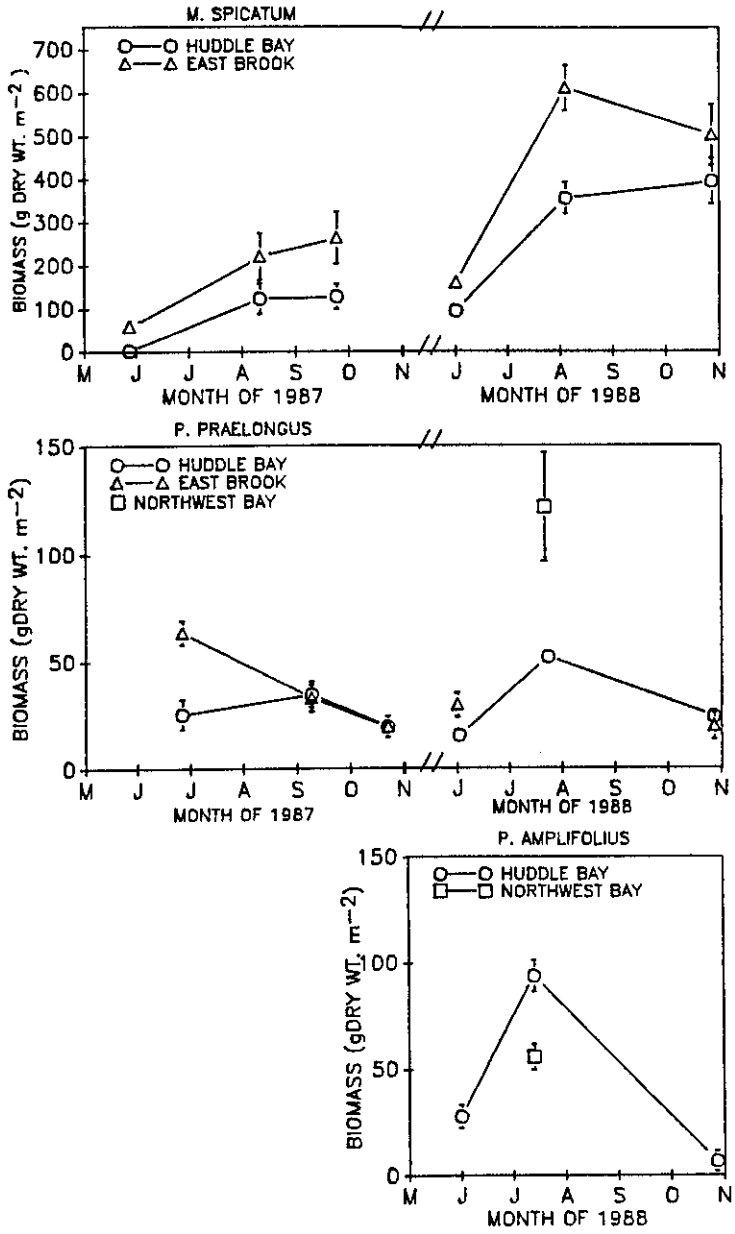


Figure 2-11. Biomass allocation to leaves and stems as percent of total dry weight for M. spicatum at East Brook and Huddle Bay during 1987 and 1988.

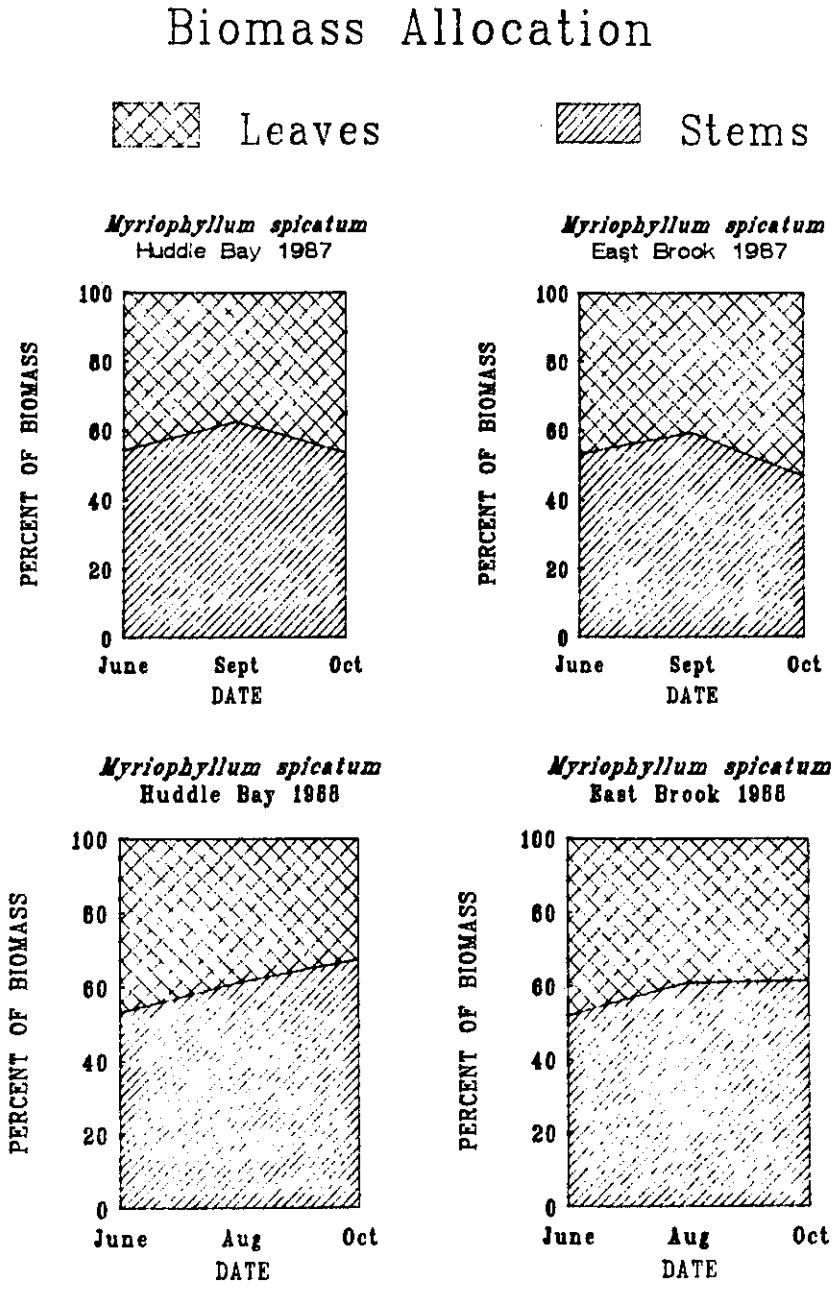


Figure 2-12. Biomass allocation to leaves, stems, and flowers as percent of total dry weight for P. praelongus at East Brook and Huddle Bay during 1987 and 1988.

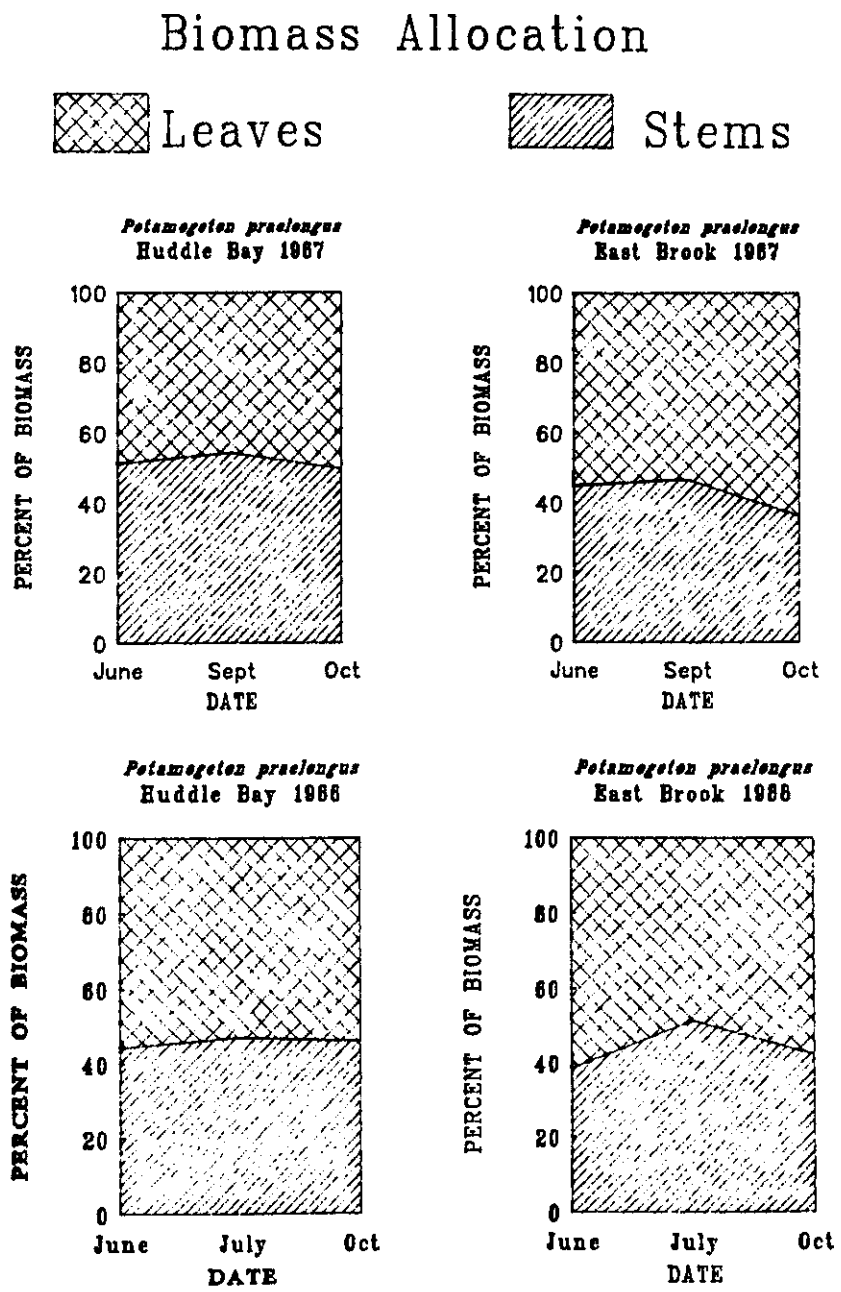


Figure 2-13. Biomass allocation to leaves, stems and flowers as percent of total dry weight for P. amplifolius at Northwest Bay Brook and Huddle Bay during 1987 and 1988.

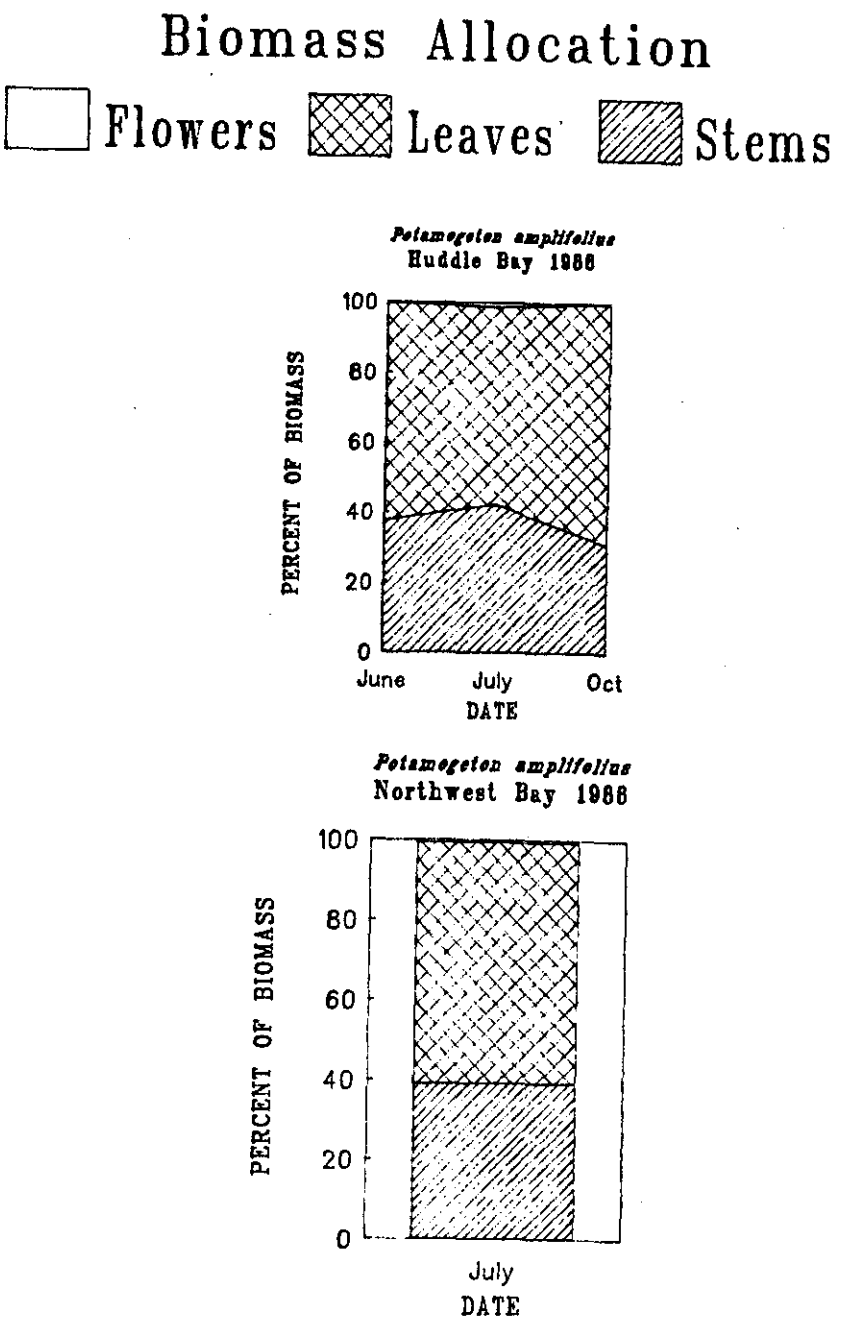


Figure 2-14. Distribution of total biomass between stems, leaves and flowers at 0.5 m height intervals for M. spicatum at East Brook and Huddle Bay during 1988.

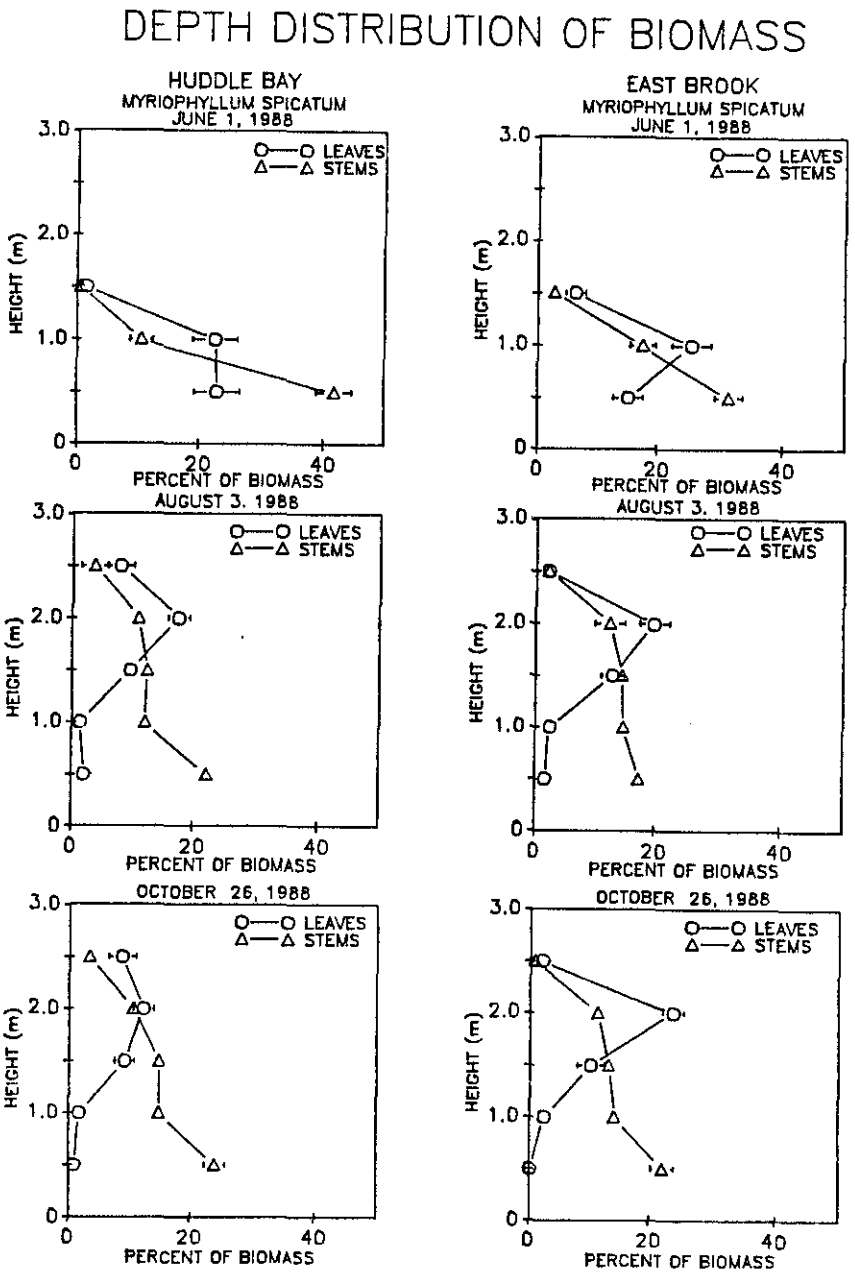


Figure 2-15. Distribution of total biomass between stems, leaves and flowers at 0.5 m height intervals for P. praelongus at East Brook and Huddle Bay during 1988.

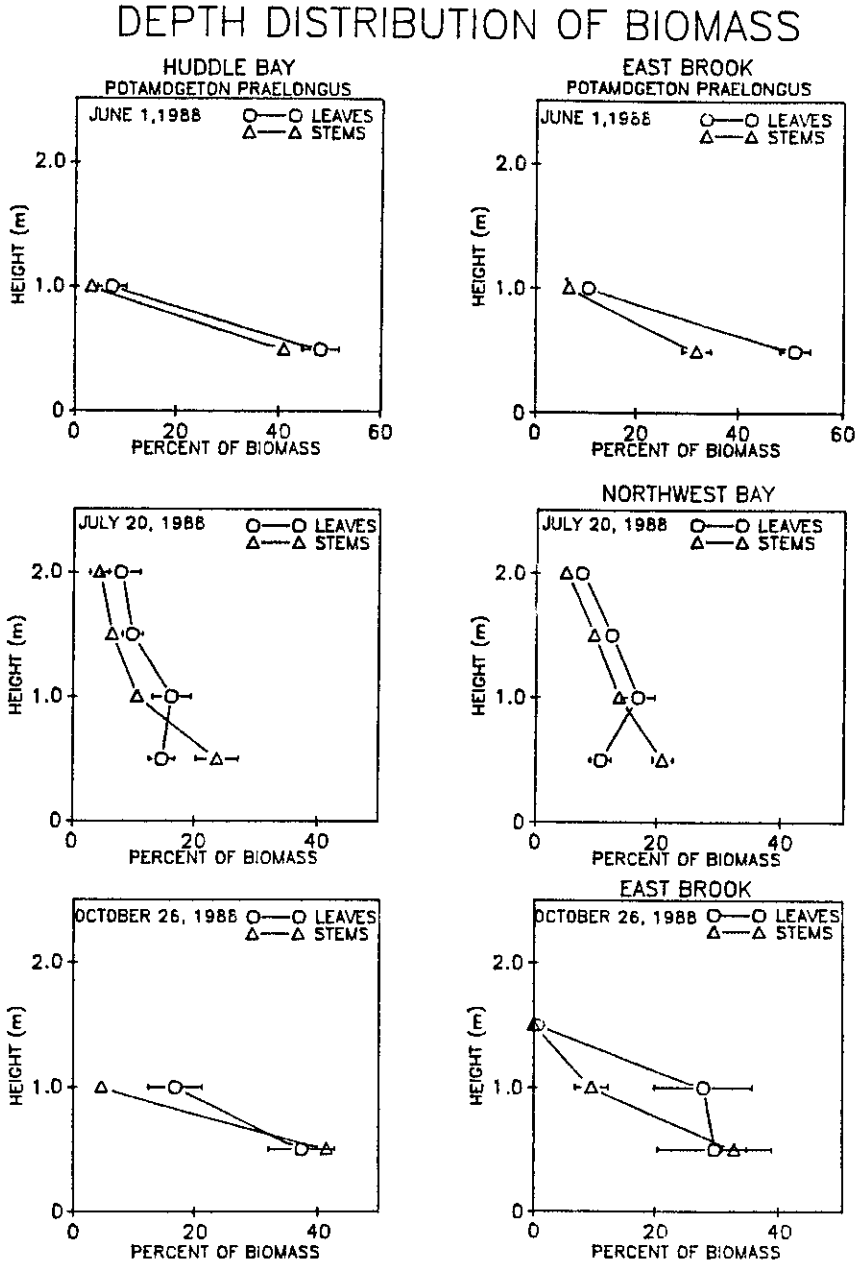
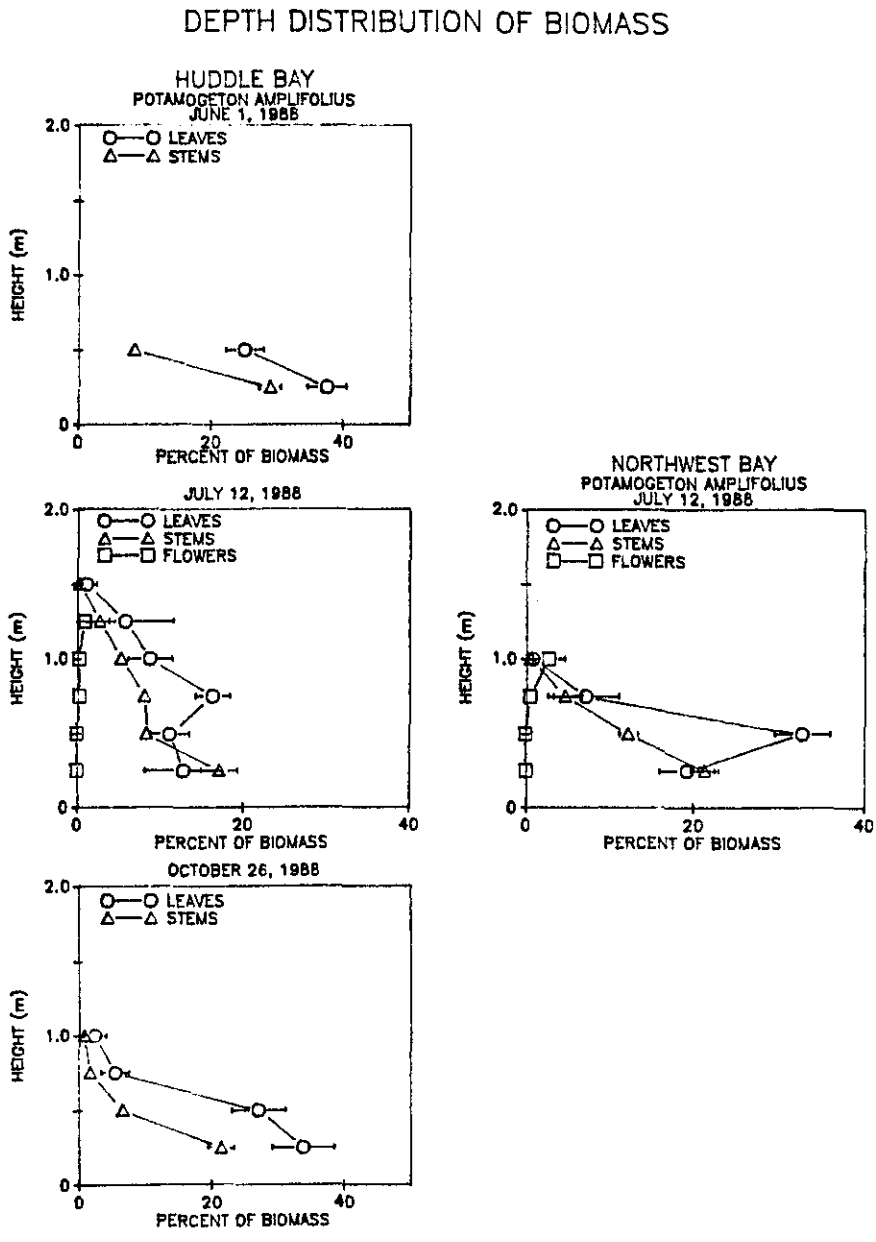


Figure 2-16. Distribution of total biomass between stems, leaves and flowers at 0.25 m height intervals for P. amplifolius at Northwest Bay Brook and Huddle Bay during 1988.



CHAPTER 3

IN SITU PHOTOSYNTHESIS

Introduction

Primary productivity of aquatic plants has been measured using many methods, both direct and indirect. Direct methods would include biomass estimates at regular intervals, with some attempt to measure plant loss or turnover by leaf tagging (Boston and Adams, 1987), leaf scar analysis (Carpenter, 1980), or measurement of senesced material (Dawson, 1976). Indirect methods would include both laboratory or shipboard methods of calculation based on photosynthetic experiments, and expressed as a mathematical model (Titus et al., 1975), or in situ measurements requiring less mathematical input (Madsen and Adams, 1988). Optimally, all three methods should be used to gain a balanced presentation of primary productivity.

In situ productivity studies generally involve stem portions that are incubated for time periods longer than most laboratory experiments. Often, these studies integrate environmental conditions encountered over a large time span, such as temperature variations, changes in sun angle and light intensity, and variations of weather patterns. As such, they often more realistically simulate actual plant conditions than most laboratory experiments, but also incorporate less experimental controls than found in the laboratory.

In situ photosynthesis is limited by available light, a parameter varied by incubation at different depths. Three important characteristics can be measured using in situ methods. Dark respiration is measured by oxygen decreases in darkened incubation bottles ("dark bottle"). Light compensation point is determined where no net oxygen change occurs in the uncovered ("light") incubation bottles, since dark respiration and gross photosynthesis are balanced. The saturation point of photosynthesis with respect to light is exhibited when no net increase in photosynthesis is observed with increased light intensity, or decreased depths of incubation.

In our in situ photosynthesis experiments, our goal was to provide real-world conditions and examine

photosynthesis of stem segments as opposed to individual leaves as in the laboratory experiments (Chapter 4). These experiments were performed as an independent check on laboratory photosynthesis.

Methods and Materials

In situ photosynthesis of aquatic macrophytes was examined by measuring the change in oxygen concentrations within 300 ml Winkler bottles over the incubation period. Oxygen concentrations were measured either utilizing modified Winkler titrations (Madsen and Adams, 1988), or using a Yellow Springs Instruments (YSI) Model 54 oxygen meter and bottle probe. In the latter case, the meter and probe were calibrated each morning. Plants used in incubations were collected from Huddle Bay. Initially, Huddle Bay was used for incubations; however, later incubations were performed at Northwest Bay Brook, Northwest Bay-West Tongue Mountain, and Paradise Bay. The latter sites were selected for greater shelter from wind and wave action.

Plant species examined were the two native pondweeds Potamogeton amplifolius and P. praelongus, and the exotic watermilfoil, Myriophyllum spicatum. Plant specimens for incubations were collected the morning of each incubation, and stored in a cooler with water to prevent drastic changes in temperature regime or overexposure to light. For each incubation, small segments of plant stem with healthy leaves were selected, for a dry matter range of 0.1 to 0.3 g dw. Plants were incubated in 300 ml dissolved oxygen/Winkler bottles, with ambient lake water used. Plants were incubated at 1, 2, 3, 4, and 5 meters depths, with six plant replicates for each depth, and two blank replicates. Typical incubation times for these depths were two hours for 1 and 2 meters depth, 3 hours for 3 meters, 4 hours for 4 meters, and 5 hours for 5 meters. In addition, two samples were collected for initial oxygen concentrations before each incubation. Also, one set of darkened bottles ("dark bottle") were incubated for six hours, with six plant replicates and two blank replicates.

In addition, environmental parameters were measured at 15- 30 minute intervals during the course of the incubations. Environmental parameters measured were profiles of light intensity and water temperature at 1 meter depth intervals, from 1 meter to 5 meters. Water temperature was measured using either a YSI

thermistor-thermometer, or the thermistor from a YSI Model 54 dissolved oxygen meter and submersible dissolved oxygen probe. Light intensity was measured as PAR quanta using a Li-Cor model 1000 light meter, with a surface quantum deck cell and submersible quantum probe.

Plants were dried overnight at 70 C, and weighed. In addition to oxygen exchange per unit dry weight and time, carbon exchange was calculated using a photosynthetic quotient of 1.2 and a respiratory quotient of 1.0 (Madsen and Adams, 1988; Wetzel and Likens, 1979).

Incubations were made during three time periods of the growing season: early (June), mid-season (September), and late (November), as indicated in Table 3-1.

Results and Discussion

Environmental conditions during each *in situ* incubation are shown in Figure 3-1. The lack of temperature data on June 24 was due to equipment malfunction. Light conditions were near-optimal for *in situ* experiments in June, were highly variable for two of the three dates in September, and far below optimal in November. Although this may point out one drawback of *in situ* measurements, namely the lack of control over environment, such environmental variability is also clearly an important element for the annual survival of plant species.

In situ photosynthesis results in terms of oxygen exchange for June are shown in Figure 3-2. The low photosynthetic rates observed for *P. amplifolius* may be due to overstocking of incubation bottles, resulting in carbon depletion. However, it may also be related to the annual productivity cycle of this species. This was the first time *in situ* incubations were performed on *P. amplifolius*. Photosynthesis of *P. praelongus* demonstrated nearly equivalent photosynthesis from 2 to 5 meters depth, with reduction in photosynthesis at 1 meter. This reduction may be due to photoinhibition. Photosynthesis of *M. spicatum* was similar from 1 to 3 meters, with significant reductions at 4 and 5 meters, a clear indication of the light-dependence of photosynthetic rates. Examining the photosynthetic rates versus light intensities, it was quite clear that *P. praelongus* exhibited a lower compensation point than *M. spicatum*, photosynthesis was saturated with respect to light at these intensities, and it exhibited a lower maximum rate of photosynthesis than the exotic watermilfoil. The graphs of photosynthesis versus depth

give an impression of the depth relationships of these species, but the graphs of photosynthesis versus light intensity are better for comparative purposes since light intensities vary from one day or incubation to the next.

In situ incubations for September are indicated in Figure 3-3. As in June, the photosynthesis of P. praelongus varied little from one to 5 meters depth, or from low to high light. Myriophyllum spicatum and P. amplifolius exhibited very similar photosynthetic rates from 1 to 5 meters, as well as when compared to ambient light concentrations.

In situ photosynthetic rates for November are shown in Figure 3-4. Once more, P. praelongus exhibits a slight, linear increase in photosynthesis from 5 to 1 meter depth, but in this case photosynthesis was not saturated. As seen from the plot of photosynthesis versus light intensity, light levels were extremely low on this date. Photosynthesis increased linearly throughout this range, and this species also exhibited the lowest compensation point of the three examined. Potamogeton amplifolius exhibited a more rapid increase in photosynthesis than M. spicatum, with a lower saturation point with respect to light. As with P. praelongus, these are shade-tolerant (or low-light tolerant) characteristics relative to M. spicatum, which has a slower rise in photosynthetic rate, and a higher saturation point. These results are consistent with those found in laboratory experiments (Chapter 4; Madsen, Hartleb and Boylen, 1989).

Using the in situ oxygen exchange data, converting these values to carbon exchange, and using appropriate calculations, the daily projected carbon balance for these three species during the three experimental periods was be calculated. A more in-depth discussion of carbon-balance simulations is presented in Chapter 4. However, it should be stressed that these carbon balance simulations are quite simplistic and are mostly useful for comparative evaluations rather than predictions of annual productivity or success.

In Figure 3-5, the daily carbon balance is presented as a function of incubation depth. Note that for each period, the change in carbon balance for P. praelongus was relatively slight, as might be expected for a shade-tolerant plant from deeper waters. The relative change in carbon balance for P. amplifolius and M. spicatum, both from

shallower habitats, was much greater at each time period.

In Figure 3-6, the daily carbon balance of these species is presented as a function of ambient light intensity at the incubation depths. In June and November, P. praelongus required the least light to maintain carbon balance, followed by M. spicatum and P. amplifolius. This order is consistent with that observed for the depth distribution of these species in Lake George (Chapter 1).

Conclusions

In situ photosynthesis experiments generally support previous findings that M. spicatum has higher maximum photosynthetic rates than native species, but it requires higher light levels to compensate respiration and to saturate photosynthetic rates. Also, M. spicatum exhibited a positive carbon balance at some temperatures throughout the growing season, as might be expected of a plant that has been observed to increase in biomass from June through October in Lake George (Madsen et al., 1989). Potamogeton praelongus exhibited traits expected of deeper-ranging plants from low light environments, less sensitivity to changes in light intensity and the lowest light compensation and saturation points. Potamogeton amplifolius had greater responses to light intensity changes, as expected of a shallower-environment species, but still had lower photosynthetic maxima than M. spicatum. Both the slope and order of carbon balance equations support community observations of the depth ranges of these species, with P. amplifolius occupying the shallowest habitats, followed by M. spicatum and P. praelongus in progressively deeper habitats. However, exact calculations of expected depth ranges based strictly on physiological measurements were more difficult to make from the present information, since the relative importance and allocation to other structures is not known.

Table 3-1. *In situ* photosynthesis experiments performed in Lake George.

NOMINAL MONTH	INCUBATION DATE	SPECIES	WATER T (C)	WINKLER OR PROBE
JUNE	14-Jun-88	M. spicatum	17	WINKLER
JUNE	23-Jun-88	P. praelongus	20	WINKLER
JUNE	24-Jun-88	P. amplifolius	--	WINKLER
SEPTEMBER	06-Sep-88	P. praelongus	22	PROBE
SEPTEMBER	07-Sep-88	M. spicatum	22	PROBE
SEPTEMBER	09-Sep-88	P. amplifolius	20	PROBE
NOVEMBER	21-Oct-88	M. spicatum	12	PROBE
NOVEMBER	01-Nov-88	P. praelongus	9	PROBE
NOVEMBER	03-Nov-88	P. amplifolius	9	PROBE

Figure 3-1. Temperature (C) and light intensity (umol m^{-2} s^{-1}) profiles for dates on which <u>in situ</u> incubations were performed.

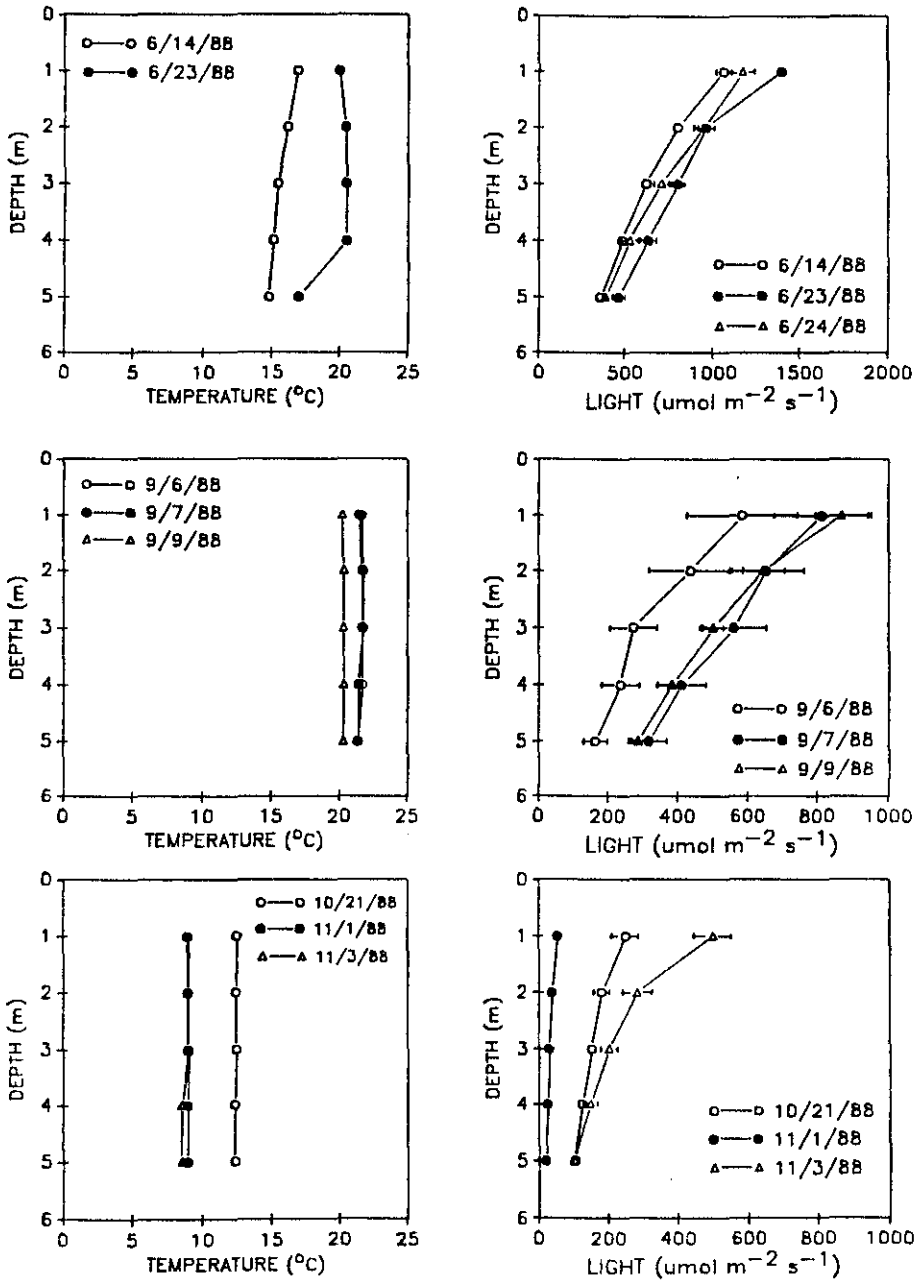
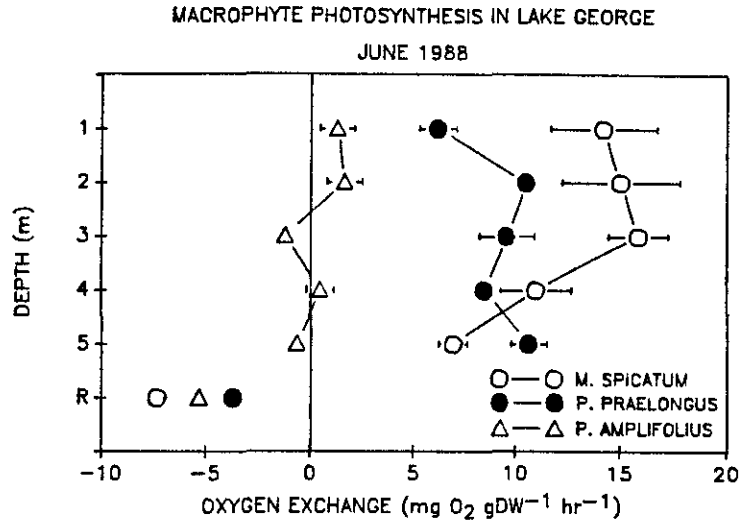


Figure 3-2. Oxygen exchange (mg O_2 g DW^{-1} h^{-1}) for depth of incubation and average light intensity at incubation depth for the three species examined in June of 1988.



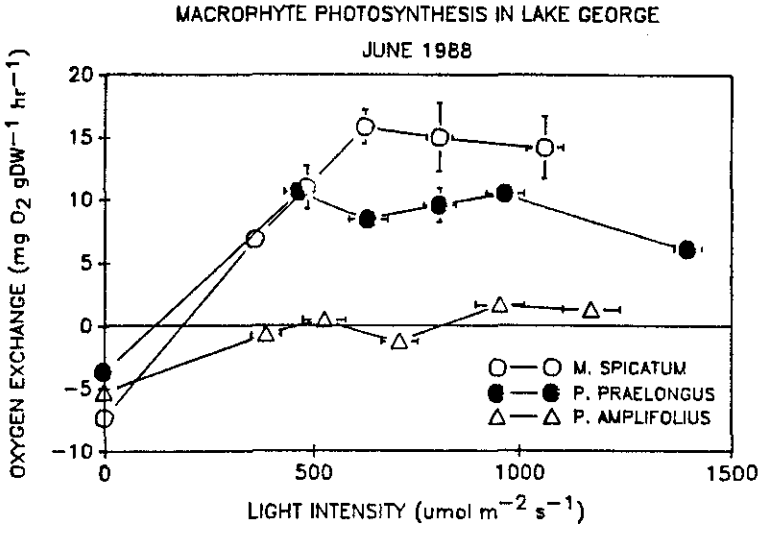


Figure 3-3. Oxygen exchange (mg O_2 g DW^{-1} h^{-1}) for depth of incubation and average light intensity at incubation depth for the three species examined in September of 1988.

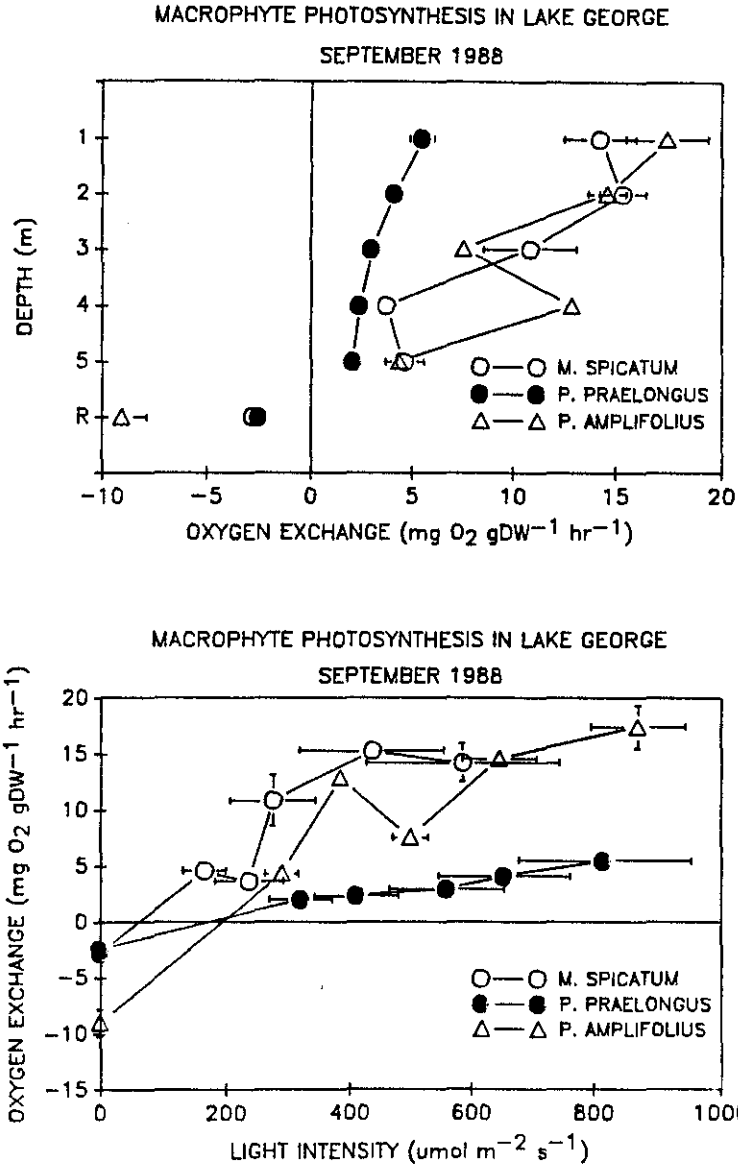


Figure 3-4. Oxygen exchange (mg O_2 g DW^{-1} h^{-1}) for depth of incubation and average light intensity at incubation depth for the three species examined in November of 1988.

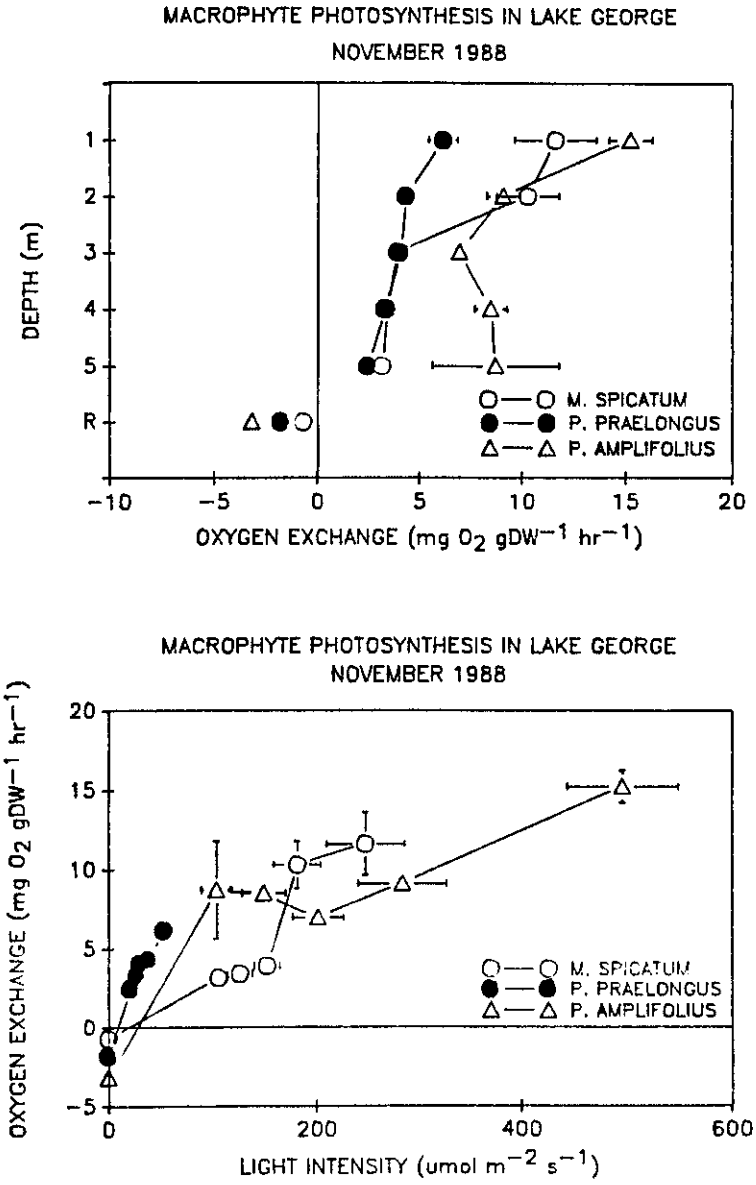


Figure 3-5. Daily carbon balance (mg C g DW^{-1} day^{-1}) versus depth (m) of incubation for the three species examined during the three experimental periods.

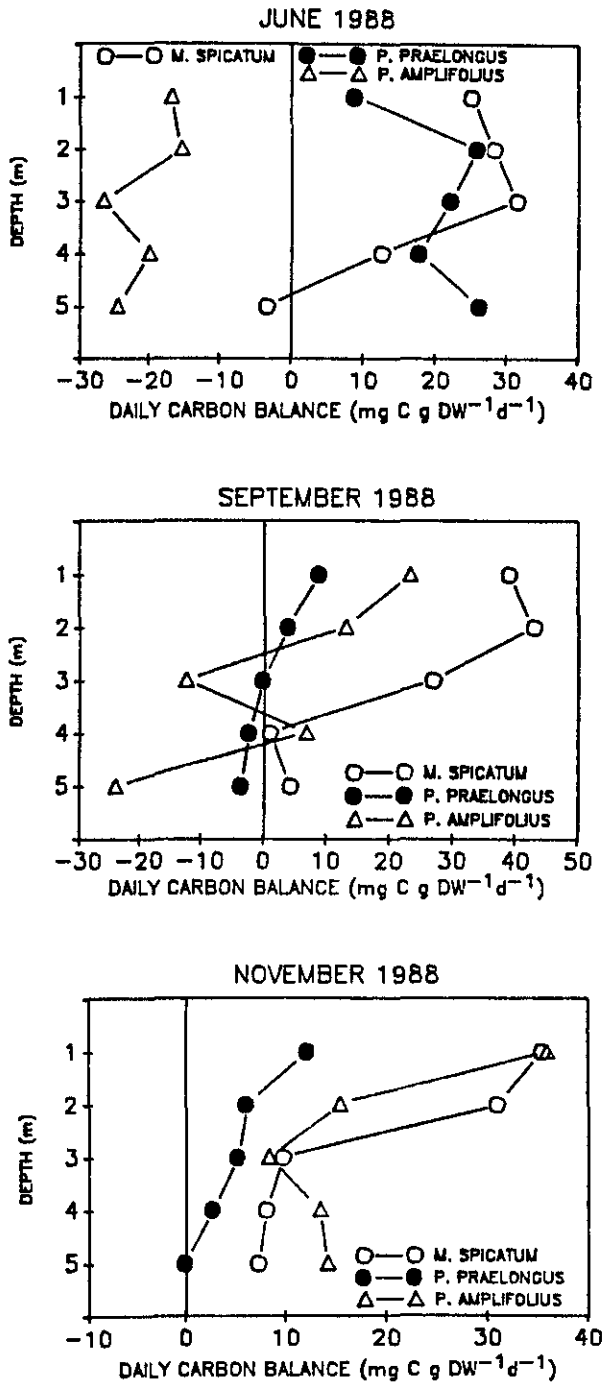
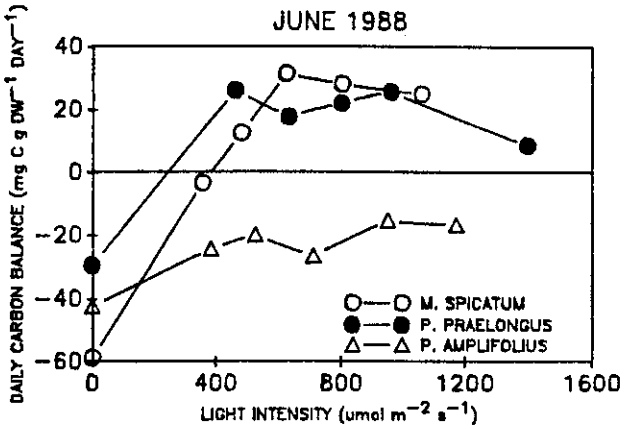
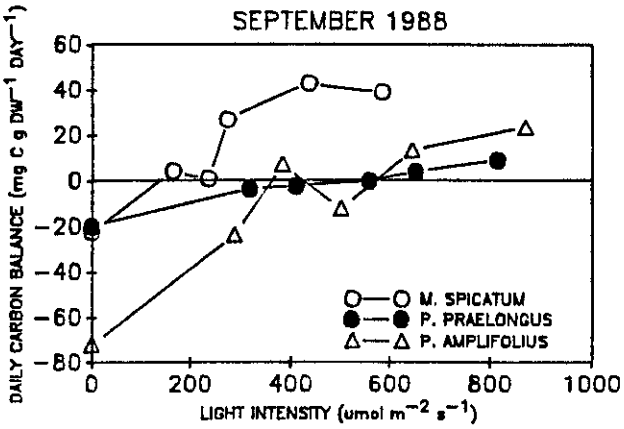
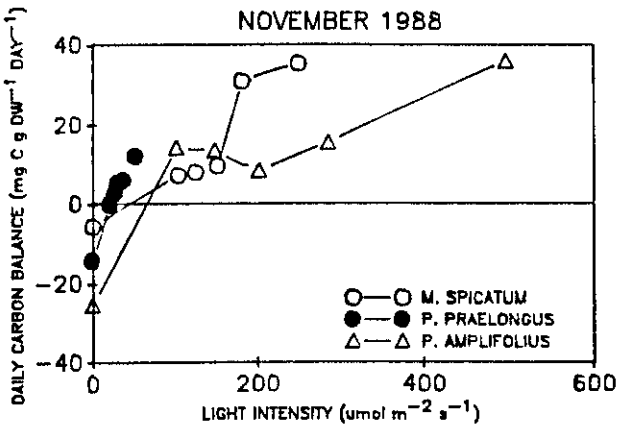


Figure 3-6. Daily carbon balance (mg C g DW^{-1} day^{-1}) versus light intensity (umol m^{-2} s^{-1}) of incubation for the three species examined during the three experimental periods.







CHAPTER 4

LABORATORY PHOTOSYNTHESIS

Introduction

Photosynthesis is one parameter often used to evaluate the relative success or competitive ability of plants in different environments. However, the maximum photosynthetic rate alone is not the only parameter of interest. The plant's ability to use low light levels, compensation point, relative light saturation point, and total carbon balance are all parameters that give some insight to a plant's capability to survive or compete in a given environment.

The photosynthetic response of a plant to light intensity has been mathematically expressed using several methods. One effective modeling technique is the use of multiple linear regression (Spencer et al., 1985). However, this approach suffers from two detractions: 1) the components within the regression equation generally do not have any biological significance, and 2) since the photosynthetic measurements in many experiments are replicated for the same specimen at several light levels, the points are not truly independent, and thus pseudoreplication may occur (Hurlbert, 1984). A better approach is to utilize a mathematical expression that has biologically-meaningful components. An example of this is the photosynthesis-irradiance relationships initially described by Talling (1957), but now has more mathematical rigor (Bulthuis, 1987). However, these equations have not resolved the problem of pseudoreplication.

Another approach is to use Michaelis-Menten kinetics to derive independent estimates of photosynthetic parameters of maximum photosynthesis (V_{max}), saturation (Km, or half-saturation constant), and dark respiration (R) that can be used in parameteric statistical analyzes or models without pseudoreplication (Madsen, 1986; Madsen and Adams, 1990). The resulting parameters are also of comparative value. This methodology was successfully used to compare Eurasian Watermilfoil to six native species in Lake George (Madsen, Hartleb and Boylen, 1989).

Several methodologies also are used to measure photosynthetic rates in aquatic plants. Most commonly,

^{14}C incorporation has been used, with several variations in technique (Lewis et al., 1982; Filbin and Hough, 1984). Although this method is often necessary, due to the low activity of some plants, it has the tendency to give highly variable results. Another excellent method, largely restricted to the laboratory, is measuring carbon gas exchange or DIC depletion (Titus et al., 1979; Madsen and Adams, 1990). However, this equipment is expensive, not generally portable, and often difficult to use to provide consistent results. Lastly, and most commonly, photosynthesis has been measured by changes in oxygen concentration in the liquid or gas phase (Agami et al., 1980; Madsen, Hartleb and Boylen, 1989). This equipment is very sensitive, is available in both laboratory and field-grade units, and is generally less expensive than carbon (or CO_2) analyzers. Although some concern has been raised about gas storage in lacunae of plants in relation to oxygen methods, this problem would be relevant to all three general methods. Some work indicates that oxygen exchange between plants and water is actually quite rapid (Westlake, 1978).

In Figure 4-1, a typical curve of photosynthetic rate versus light intensity is presented to demonstrate four basic characteristics of photosynthetic curves. The first characteristic represented is the dark respiration rate, which is the rate of oxygen consumption or carbon loss from the plant tissue in the absence of light. The respiration rate represents the basic metabolic overhead, or cost, of the plant tissue examined. The second characteristic exhibited is the light compensation point, defined as the light level at which gross photosynthesis equals the dark respiration rate, or net photosynthesis (carbon exchange) is zero.

The slope and height of the photosynthetic curve is dependent on two additional characteristics, variously defined dependent on the model used. Since we have employed a Michaelis-Menten model to characterize photosynthesis, the two model parameters we will use are the Michaelis-Menten parameters V_{max} and Km. The maximum photosynthetic rate, V_{max}, expresses the asymptote the curve approaches, or ideal maximum rate given infinite substrate (in this case, light). The other parameter, Km, is the half-saturation constant of photosynthesis with respect to light. This parameter determines how rapidly the photosynthetic rate approaches V_{max}, or the efficiency with which plants utilize light. It is a measure of the amount

of light required to maximize photosynthesis.

Methods

The species examined were two native pondweeds, Potamogeton amplifolius and P. praelongus, and the exotic watermilfoil Myriophyllum spicatum. The reasons for selecting these species are discussed in Chapter 1. Experimental plant shoots (eight to twelve per sample period) were collected from Huddle Bay, Lake George (see Chapter 2). Myriophyllum spicatum shoots were selected from 3 meters depth, P. amplifolius from 2 meters depth, and P. praelongus from 4 meters depth.

Plants were collected at times so that environmental (lake water) temperatures corresponded with treatment temperatures. Plants were returned to the laboratory, and maintained at the treatment temperature using a cooling/heating unit in aquaria. Light was maintained at 200 umol m^{-2} s^{-1} at the ambient photoperiod.

Photosynthesis was examined using a Yellow Springs Instruments model 5300 Biological Oxygen Monitor to measure short-term oxygen exchanges (5-30 minutes) over a range of eight light intensities from 0 to 1000 umol m^{-2} s^{-1} at 15 C, 20 C, and 25 C, with six to eight replicates at each temperature for each species. Oxygen exchange rates were converted to carbon exchange using a respiratory coefficient of 1.0, and a photosynthetic coefficient of 1.2. Gross photosynthesis was modeled for light intensity using an iterative Michaelis-Menten equation to derive V_{max} (maximum rate of photosynthesis) and Km (half saturation constant for light intensity). Respiration rates were utilized to calculate photosynthetic light compensation points from Michaelis-Menten constants.

Results and Discussion

In Figure 4-2, the oxygen exchange rates versus light intensity of all three species for the three experimental temperatures is presented. Myriophyllum spicatum appeared to have its peak net photosynthetic rate at both 15 C and 20 C, with greatly reduced photosynthesis and much higher light compensation point at 25 C. Since the collection times of these plants was greatly separated in time, these differences could be as much due to seasonal shifts in photosynthetic activity as to temperature dependence.

Potamogeton praelongus had virtually identical photosynthesis versus irradiance curves for all three temperatures. Potamogeton amplifolius exhibited very similar photosynthesis versus irradiance curves for 15 C and 25 C, but substantially higher rates of photosynthesis at 20 C. This difference was probably attributed to decreased activity at both cold temperatures, and under a senescence period during the warmest temperatures.

V_{max} versus temperature is presented in Figure 4-3. Myriophyllum spicatum exhibited its highest V_{max} at 20 C, a typical surface temperature for Lake George. V_{max} was considerably lower at both 15 C and 25 C. A similar pattern was observed for P. amplifolius, except that the maximum V_{max} (1.4 mg C g DW^{-1} h^{-1}) was significantly below that for M. spicatum (2.2 mg C g DW^{-1} h^{-1}). Potamogeton praelongus maximum V_{max} was observed at 15 C, with a linear decrease at higher temperatures.

The data in Figure 4-4 is presented with the Y-axis being negative, with increasing amplitude going from top to bottom as a convention for calculations, and because respiration is defined as carbon loss or oxygen consumption. Although respiration rates generally increase with increasing temperature, in both Potamogeton species the opposite was observed; namely, that respiration rates decreased at higher temperatures (Figure 4-4). However, since the plants were sampled at different times, this may indicate plant acclimation or enzymatic change during the growing season. For instance, these two species typically grow within a narrow time frame of June through mid-July, after which senescence occurs. Plants may have been sampled at a time when the species were not as active. In contrast, respiration rates increased with increasing temperature for M. spicatum, as would be expected.

The Km for all three species was similar at 15 C; but Km remained linear for the two Potamogeton species, decreasing slightly, while Km increased dramatically for M. spicatum, from 39 at 15 C to 98 at 20 C and 77 at 25 C (Figure 4-5). Myriophyllum spicatum utilized much more light at higher temperatures, while the two Potamogeton species exhibited more typical shade-tolerant attributes (Madsen, Hartleb and Boylen, 1989).

The light compensation point is the light value at

which gross photosynthesis equals respiration, or net photosynthesis is zero. This is an instantaneous measure, and does not consider that daily carbon balance must include both a dark period of respiration alone. In Figure 4-6, compensation point for the three species is indicated as a function of temperature. Note that again, compensation point for the two Potamogeton species decreased with temperature, due to the previously discussed change in respiration. However, compensation point for M. spicatum increased dramatically with temperature. In this parameter as well, the two Potamogeton species exhibited shade-tolerant characteristics, while M. spicatum exhibited a compensation point more typical of high-light requiring plants, or a canopy species adapted to a high-light environment.

The photosynthetic response surface of M. spicatum exhibited a relatively flat response to temperature, with a peak at 20 C (Figure 4-7). However, this rather low temperature maximum may be a function of the low-temperature environment in Lake George, with water temperatures barely exceeding 20 C, and rarely reaching 25 C. In comparison, the response surface of P. amplifolius was more sharply peaked at 20 C, but with a lower maximum photosynthetic rate (Figure 4-8). Potamogeton praelongus exhibited a similar maximum rate to the other Potamogeton species, with a less defined peak of activity at 20 C (Figure 4-9). These response surfaces are unusual compared to other species, in that the maximum rate was found at 20 C. For instance, Madsen and Adams (1990) found a maximum rate at 28 C for P. pectinatus, but that was for an environment with a higher temperature range. Optimal temperatures for photosynthesis of M. spicatum from Lake Wingra, a much warmer eutrophic lake, ranged from 25 C (Adams and McCracken, 1974) to 33.6 C (Titus and Adams, 1979).

Utilizing the Michaelis-Menten parameters measured above, simplistic carbon balance equations were calculated to evaluate the relative ability of these species to function in the lake environment. Two such scenarios were examined. In each, a 14-hour day was estimated, as is typical of the summer. Equations from each temperature were plotted, using actual measured light intensity profiles from the lake, collected on a clear day. These models are quite simplistic in their assumptions. First, light levels were not varied over the day, though a certain amount of daylength was deducted from the beginning and end of each day to account for sunrise and sunset. Second,

photosynthetic rates were not varied over the day, although some studies suggest that this in fact occurs (Adams and McCracken, 1974). Third, respiration was held constant, although some evidence suggests that different plant organs and different time of day may alter respiratory activity. Last, no attempt was made to incorporate the respiratory load of nonphotosynthetic tissues, although this may well be critical to an in-depth evaluation of plant carbon balance. For instance, M. spicatum has more allocation to nonphotosynthetic stems than either Potamogeton species. Both have a significant investment into subsediment rhizomes and roots.

In the first scenario, a light profile from the open water was utilized (Figure 4-10). At 25 C, M. spicatum was unable to maintain a positive carbon balance. However, significant carbon gains were realized at 15 C and 20 C to a depth of 10 meters. Note the rapid decrease (slope) in carbon gain at 20 C relative to the other species. Potamogeton amplifolius carbon gain was throughout the water column at 20 C and 25 C, but only in the upper 3 meters at 15 C. Stored carbohydrates may be utilized to survive difficult periods, but likewise critical times, such as cold temperature periods, may be limiting to the survival of these species. For instance, measured net primary productivity in Badfish Creek showed that P. pectinatus could not maintain a positive carbon balance during time periods when water temperatures were below 15 C (Madsen and Adams, 1988). Potamogeton praelongus exhibited a similar pattern to P. amplifolius, except that depth at which carbon balance approached zero was 6 meters. Interestingly, these values approximate the typical depth limits of these two Potamogeton species in Lake George (see Figure 1-2).

In the second scenario, a light profile was utilized from a dense M. spicatum bed, in which the upper part of the canopy was found at a depth of approximately 0.5 meters (Figure 4-11). Myriophyllum spicatum was unable to maintain positive carbon balance at 25 C, and maintains positive carbon balance only in the upper 1 meter of the water column at 15 and 20 C. Self-shading in a M. spicatum canopy is intense, and accounts for the sloughing of leaves in the lower part of the canopy. Likewise, the two native species can only maintain a positive carbon balance in the upper 1 meter of the water column, and cannot maintain positive carbon balance below the canopy. This substantiates the paucity of native plants observed below the dense M.

spicatum canopies in Lake George (Madsen et al., 1989), and provides at least one mechanism for the dominance of M. spicatum over native plants; namely, shading of native species and subsequent reduction in primary productivity. Of course, other factors may also contribute to the dominance of M. spicatum over native species.

Conclusions

Myriophyllum spicatum exhibited a higher V_{max} and Km than the two native Potamogeton species, at least at 20 C and 25 C. Photosynthetic characteristics of all three species were quite similar at 15 C. All three species exhibited maximum photosynthesis at 20 C. The native species exhibited shade-tolerant attributes, while M. spicatum exhibited attributes more typical of a high-light, competitive canopy species. Simulated carbon balance scenarios indicated some possible mechanisms for the depth limitation of the two native Pondweeds, and also indicated the rapid attenuation of the maintenance of carbon balance by M. spicatum, demonstrating its sensitivity to light levels. A carbon-balance scenario based on a light profile through a M. spicatum canopy demonstrated that significant self-shading will occur, and the dense canopy will restrict light levels sufficient to limit the growth of native plants.