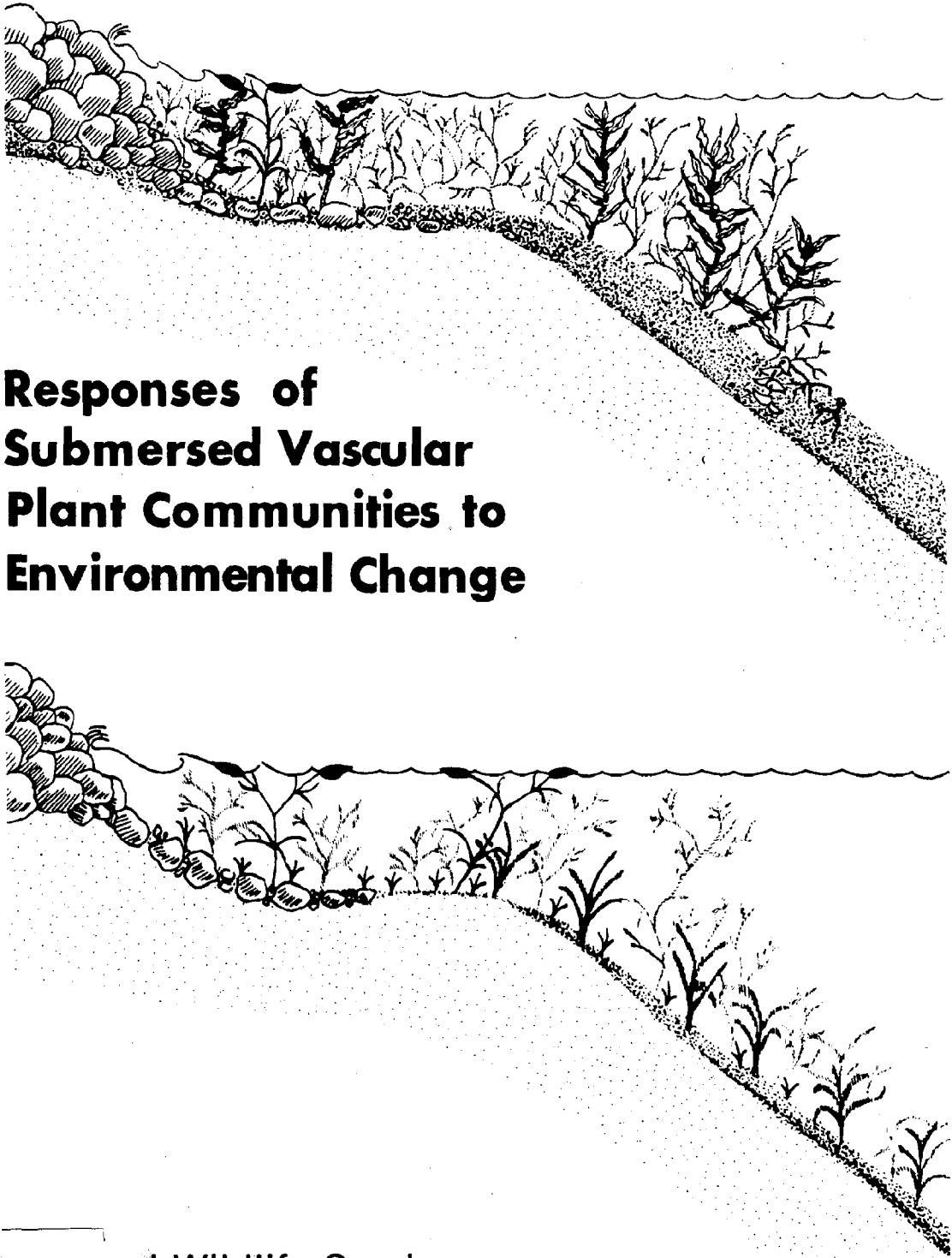


Biological Services Program

FWS/OBS-79/33
August 1980



Responses of Submersed Vascular Plant Communities to Environmental Change

and Wildlife Service

Department of the Interior

QK930
.D38
R47
1980

The Biological Services Program was established within the U.S. Fish and Wildlife Service to supply scientific information and methodologies on key environmental issues that impact fish and wildlife resources and their supporting ecosystems.

Projects have been initiated in the following areas: coal extraction and conversion; power plants; mineral development; water resource analysis, including stream alterations and western water allocation; coastal ecosystems and Outer Continental Shelf development; environmental contaminants; National Wetland Inventory; habitat classification and evaluation; inventory and data management systems; and information management.

The Biological Services Program consists of the Office of Biological Services in Washington, D.C., which is responsible for overall planning and management; National Teams, which provide the Program's central scientific and technical expertise and arrange for development of information and technology by contracting with States, universities, consulting firms, and others; Regional Teams, which provide local expertise and are an important link between the National Teams and the problems at the operating level; and staff at certain Fish and Wildlife Service research facilities, who conduct inhouse research studies.

15691

FWS/OBS-79/33
August 1980

**COASTAL ZONE
INFORMATION CENTER**

RESPONSES OF SUBMERSED VASCULAR PLANT COMMUNITIES
TO ENVIRONMENTAL CHANGE

by

Graham J. Davis and Mark M. Brinson
Department of Biology
East Carolina University
Greenville, North Carolina 27834

Contract No. 14-16-0009-78-032

Project Officer

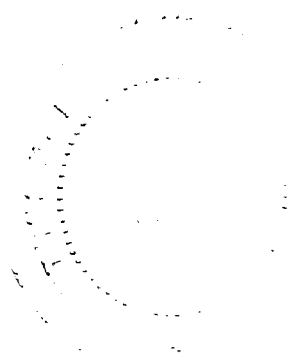
Charles Segelquist
Eastern Energy and Land Use Team
Route 3, Box 44
Kearneysville, West Virginia 25430

Property of CSC Library

Performed for:
Eastern Energy and Land Use Team
National Water Resources Analysis Group
Office of Biological Services
Fish and Wildlife Service
U.S. DEPARTMENT OF THE INTERIOR

US Department of Commerce
NOAA Coastal Services Center Library
2234 South Hobson Avenue
Charleston, SC 29405-2413

U.S. Dep. of the Interior. Fish and Wildlife Service
MAY 20 1997



LIBRARY OF CONGRESS

Library of Congress Catalog Card Number: 80-607178

REPRODUCED FROM THE
ORIGINAL MANUSCRIPT
OF THE
LIBRARY OF CONGRESS
80-607178

PREFACE

Many construction activities in or near streams and lakes cause changes in the aquatic environment that affect submersed vascular aquatic plants. This report was prepared to give biologists, engineers, and planners an overview of how submersed plants respond to changing environmental conditions including light transmission, fluctuating water levels, currents and waves, and other physical and biotic factors.

A companion document, FWS/OBS-80/42, is a summary of this technical report. Inquiries concerning the availability of either report should be directed to:

Information Transfer Specialist
U. S. Fish and Wildlife Service
Eastern Energy and Land Use Team
Route 3, Box 44
Kearneysville, West Virginia 25430

EXECUTIVE SUMMARY

Submersed vascular plants are native to many aquatic ecosystems where they influence a number of ecosystem processes and provide food and shelter for fish and wildlife. This report examines factors that affect the light environment of submersed macrophytes and evaluates the responses of submersed plant communities to changing light conditions. Other requirements and stresses important to submersed macrophyte communities are discussed also.

The amount of light available for photosynthesis and growth of submersed plants depends on the combination of the turbidity of the water and the depth at which they grow. Turbidity due to suspended sediments may vary greatly depending on the energy of currents and waves that keep them in suspension or on human activities that may create new sources of particulate matter. Deposition of sediments directly on leaf surfaces may reduce light available to plants. Increases in plankton density, matting filamentous algae, and dense epiphytic growth, all common consequences of eutrophication, can reduce the amount of light available to submersed macrophytes. Other factors affecting the survival and growth of aquatic macrophytes are grazing and feeding activities of fish and waterfowl, fluctuating water levels, hydrostatic pressure, and sediment type. All of these factors are reviewed briefly and examples given from pertinent studies.

Data were assembled on depth distribution records of submersed angiosperms and the Secchi transparencies of water for mostly North American lakes. These were lakes in which the maximum depth of submersed macrophyte establishment was limited by light availability rather than shallow depth. Although the data base lacks rigorous precision, several patterns reveal that species respond quite differently to reduced light levels with increasing depth. Laboratory and field studies generally show that most shade tolerant species have a rapid photosynthetic response to increasing light in the low range of intensities. In clear shallow waters, the competitive advantage is shifted toward species in which photosynthesis is saturated only by extremely high light intensities.

Further analysis of depth distribution patterns of species and water transparency allowed identification of turbidity tolerant and non-tolerant species. This was expressed as a turbidity tolerance index, which in turbid waters (Secchi transparency ≤ 2.5 m), is the ratio of the depth maxima of species to the Secchi transparency depth. The index ranked ten species according to their resistance to adverse effects of turbid systems.

Submersed macrophyte communities may respond differently to short term and long term perturbations. Short term changes may vary from a few weeks to a few years and usually have no lasting detrimental effects on the aquatic macrophytes. Long term changes associated with factors such as eutrophication result in elimination of species sensitive to light reduction and often in the appearance of exotic species.

Based on long term studies of northern lakes, a survival index for submersed species was developed. This index and the turbidity tolerance index were used, along with other information, to identify five groups of species that have varying degrees of resistance to ecosystem alteration.

Finally the possible effects of human activities on alterations in aquatic ecosystems and an array of impacts on submersed plant communities are considered. Since a wide range of ecosystem changes can be associated with a single type of perturbation and since responses of submersed macrophytes to system changes cannot be predicted with confidence, these impact evaluations are tentative.

TABLE OF CONTENTS

	<u>Page</u>
PREFACE	iii
EXECUTIVE SUMMARY	iv
LIST OF FIGURES	viii
LIST OF TABLES	ix
ACKNOWLEDGMENTS	x
 INTRODUCTION	 1
PHYSICAL, CHEMICAL, AND BIOLOGICAL FACTORS AFFECTING SUBMERSED	
PLANT GROWTH	3
Fluctuating Water Levels	3
Currents and Waves	4
Suspended Sediments and Their Effects on Submersed Plants	5
Growing Season and Dormancy	9
Nutrient Availability and Uptake	9
Biological Factors	10
Hydrostatic Pressure	12
RESPONSES OF SUBMERSED PLANTS TO LIGHT AND TURBIDITY	14
Light Attenuation	14
Relationship of Actual Light Transmission and Secchi Disc	
Transparency Estimates to the Euphotic Zone	15
Depth Zonation and Turbidity Tolerance of Submersed Species	17
Relationship between Maximum Depth Distribution and Secchi	
Transparency	26
Turbidity Tolerance Index	29
Photosynthesis and Growth in Response to Light	30
Laboratory Experiments	31
Field Studies	34
RESPONSES OF SUBMERSED PLANTS TO ECOSYSTEM CHANGE	35
Community Responses to the Duration of Perturbations	35
Short Term Perturbations	35
Long Term Perturbations	37
Categories of Species Based on Resistance to Ecosystem Alteration	42
Rosalate Species	43
Northern Potamogetons	43
Tolerant Species Normally with Low Biomass in Disturbed Systems	44
Tolerant Species Normally Dominant or Subdominant in Disturbed	
Systems	44
Adventive Species	45

EFFECTS OF ENVIRONMENTAL ALTERATIONS ON SUBMERSED AQUATIC PLANTS . . .	46
REFERENCES	52
APPENDICES	
A. Regions of North America that Correspond to the Distribution Codes of Appendix B	62
B. Species, Family, Common Name, and Distribution of North American Aquatic Macrophytes Mentioned in Text	63

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Comparison of settling velocities described by Stokes law and the impact law.	7
2	The relationship between current velocity and particle size which determines whether particles will be eroded, transported, or deposited	7
3	Schematic diagram of factors that contribute towards a tendency for nutrient absorption by roots or shoots	11
4	Hypothetical changes in relative primary productivity of submersed, emergent, epiphytic, and planktonic communities with increasing nutrient enrichment.	12
5	Depth maxima for aquatic vascular plants and <i>Nitella</i> spp. as related to the 1 percent light transmission depth for some British lakes.	13
6	Absorption spectra of water from Lake George, Wisconsin, compared with pure water.	16
7	Depth distributions for submersed macrophytes	18
8	Maximum depth distribution of selected species from Figure 7 plotted against Secchi disc transparency of the waters where the distributions were observed	27
9	Conceptual model illustrating the effects of environmental forces on submersed aquatic macrophyte communities.	47

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Turbidity tolerance index for selected species of Figure 7 expressed as the ratio of depth maxima to Secchi depth where Secchi depth is 2.5 m or less.	30
2	Changes in submersed macrophyte populations in Reelfoot Lake, Tennessee.	36
3	Long term changes in macrophyte populations in lakes and bays in northern United States.	38
4	Evaluation of the effects of various types of environmental alteration on submersed plant communities.	49

ACKNOWLEDGMENTS

The following persons contributed to the preparation of this manuscript: Randy Creech prepared the illustrations, Carol Lunney photographically reproduced the figures, Sue Williams and Margaret Schiller typed preliminary drafts, and Cindy Stack of the Institute for Coastal and Marine Resources typed the final copy.

The cover diagrams were drawn by Ray Moore. An attempt was made to illustrate the effects of phytoplankton turbidity on submersed plant community structure in two otherwise similar areas of eutrophic Little John Lake and oligotrophic Silver Lake in Wisconsin (after Wilson, 1935).

INTRODUCTION

There are many examples of waters that at one time supported luxuriant growths of macrophytes but are now largely devoid of these plants. The causes for the reduced abundance vary, but most are associated with increases in water turbidity. However, the absence of submersed macrophytes does not always imply that adequate light is lacking. Submersed macrophytes generally colonize high energy and rather unstable zones of lakes, reservoirs, rivers, and estuaries and are subjected to a number of stresses that may exclude them. Some of these stresses are discussed to put in proper perspective the importance of light availability. However, the main subject area of this review is the effects that reduced light availability and increased turbidity have on submersed plants in inland waters.

The probable effects that increased water turbidity might have on submersed angiosperms will be evaluated. A number of human activities such as dredging, waste disposal, boat traffic, road construction, land use, etc. may add suspended solids to lakes and rivers at levels above background. However, background or "natural" turbidity can vary greatly in rivers depending on current velocity following heavy rains or snow melt and in lakes depending on mixing by wind, bank erosion, and inflows from turbid rivers and streams. The changes in turbidity and thus the light environment of submersed macrophytes corresponding with these events need to be evaluated relative to other factors that limit macrophyte distribution. The importance of these "residuals" is often very difficult to quantify.

The importance of submersed macrophytes in aquatic ecosystems is widely recognized by biologists, but public perception of their value focuses primarily on their utilization by migratory waterfowl as food. Many aquatic vertebrates and invertebrates utilize aquatic macrophytes for food and cover. In fact, the metabolism of many flowing and limnetic ecosystems is dominated by photosynthesis and respiration of aquatic macrophytes which are at the base of the detritus food web. Exchange of nutrients among the compartments of the sediment-plant-water system and calcium carbonate precipitation in plant beds can have striking effects on the water chemistry of aquatic ecosystems.

Most of the data and examples reviewed are from North America. Examples from north-central and northeastern United States and contiguous Canadian areas dominate the review. This is due partly to the abundance of lakes in those districts and partly to the large number of limnological studies conducted there. Data are presented for areas other than North America, but a

serious review of the world literature was not made. Some of the most relevant studies on turbidity-macrophyte relationships have been conducted in shallow estuaries rather than lakes.

While the studies cited date back to the early decades of this century, many of the relevant data are of recent origin. Problems associated with overabundance of certain macrophytes (e.g., Myriophyllum spicatum, Hydrilla verticillata) have provided the impetus for some of these studies. A few investigators in the field have recently focused much of their effort toward resolving the relationship between distribution of aquatic macrophytes and water transparency. We hope that this review will provide additional insight, identify some critical gaps in our knowledge, and suggest important areas of research.

North American species mentioned in this report are listed alphabetically in the table in the Appendices with additional information on the family, common name, and distribution. Distribution is given according to the regions developed in Shelter and Skog (1978).

PHYSICAL, CHEMICAL, AND BIOLOGICAL FACTORS AFFECTING SUBMERSED PLANT GROWTH

Among the submersed vascular plants, there is great variation in life cycle, morphology, physiology, and reproduction which somewhat reflects the diversity of their terrestrial ancestors (Arber, 1920). This diversity is illustrated by the wide range of physical and chemical conditions to which various species are adapted. The species composition and abundance in a submersed plant community will depend upon the totality of these factors to which an area is subjected. The purpose of this section is to provide an overview of the importance of factors other than light which may limit the abundance, or even the occurrence, of aquatic vascular plants. While the discussion focuses on the submersed life forms, many of the factors mentioned also relate to emergent and floating leaved species.

FLUCTUATING WATER LEVELS

Fluctuating water levels are common features in many shallow aquatic ecosystems. The distribution of wetland plants in response to a drop and subsequent rise in water level in a prairie pothole marsh is illustrated in a study by van der Valk and Davis (1976). The submerged zone was completely exposed during a summer drought which almost eliminated Ceratophyllum demersum when reflooding occurred the following year. Another submersed species, Potamogeton sp. aff. pusillus, was little affected but moved 4 or 5 m closer to shore after reflooding. There was a tendency during the drought for emergent species to germinate and invade the submersed zone such that biomass and species richness of the zone increased after reflooding. This illustrates that although some submersed species are severely affected by extreme water level fluctuation (e.g., Ceratophyllum, which is not rooted), others adapt by a shift in zonation. However, considering the community as a whole, irrespective of life form, there was little overall change in community production and diversity due to water level fluctuation.

Where drawdown can be artificially controlled it is commonly used in control procedures for aquatic macrophytes. Peltier and Welch (1970) suggested that drawdown, along with low rainfall, resulted in greatly increased coverage by Najas spp. in an Alabama reservoir. Similarly, Jackson and Starrett (1959) noted that Potamogeton pectinatus grew best when water levels remained low in the shallow, floodplain of Lake Chataqua, Illinois. In the Chippewa Flowage, Wisconsin, which has received repeated winter drawdowns for 50

years, Nichols (1975) identified five submersed species that either recovered, or increased in coverage after repeated water fluctuation. On the other hand, if drawdowns are not properly conducted, problems resulting from excessive macrophyte growth may result especially in areas with long growing seasons, as predicted by Hestand et al. (1973) for Lake Ocklawaha, Florida.

Where drawdowns persist for several years or are frequent during a single growing season, as in some reservoirs, submersed vascular plants will not survive. Reservoirs typically have highly turbid waters and few shallow areas which further reduces chances for establishment of submersed vegetation. Controlled drawdowns have been used in the TVA reservoir system for management of Myriophyllum spicatum, a nuisance plant (Leon Bates, personal communication).

Submersed species may be limited in their length of growth by shallow water, but it is uncertain whether this would affect rates of production. For example, Lind and Cottam (1969) found that Myriophyllum exallescens, in Lake Mendota, Wisconsin, was about half as dense at 2.0 to 2.5 m depth as at 1 m, but the average weight per plant was about twice as great in the deeper water. Whether Myriophyllum would respond to increasing water depths during a single growing season by elongation and reduction in density is uncertain. Alternatively, reduced depths may result in greater fragmentation and uprooting from turbulence as more of the plant floats near the surface.

Martin and Uhler (1939) stated that at least a few inches of water must be retained for truly aquatic plants to remain established. Of the species that they suggested for propagation in periodically exposed wetlands, none are submersed aquatics. None of the seeds of aquatic plants mentioned by Sculthorpe (1967) that require drying before germination were from submersed species.

CURRENTS AND WAVES

In medium to large lakes the eroding forces of waves may prevent the establishment or result in the fragmentation of submersed aquatic plants in the shallowest zone. Their absence is probably more commonly due to the abrasive action of waves rather than instability of the substrates. In mature basins, the amount of erodable inorganic material in this high energy zone is usually small, having long since been removed (Hutchinson, 1975). There is a tendency for submersed vascular plants that grow in these situations to be small and their occurrence probably depends on resistance to fragmentation.

Fragmentation due to wave action was determined by Jupp and Spence (1977b) for Potamogeton filiformis in Loch Leven, Scotland. By comparing peak biomass of plots protected from wave action and waterfowl grazing (243 g/m²) with plots protected only from waterfowl grazing (125 g/m²), a loss of 118 g/m² was attributable to wave action. Since plant densities did not differ significantly between treatments, all of this loss was due to wave pruning of shoots. It is uncertain, however, to what extent fragmentation

calculated by this procedure actually occurred and to what degree wave action may have merely inhibited potential growth.

In running waters only rooted growth forms become established and thus they are restricted to areas of sediment deposition, with the notable exception of members of the mostly tropical Podostemaceae which are attached to rocks in fast flowing water (Arber, 1920). Hynes (1970a) stated that no rooted plants show any special adaptation to running water, and the species that occur in streams and rivers have tough, flexible stems or leaves, a creeping growth habit, frequent adventitious roots, and strictly vegetative reproduction.

According to Westlake (personal communication) the relationship between plant distribution, depth, light and compensation point are complex, particularly in the relatively shallow depths colonized in fairly turbid river waters. In these conditions many plants are capable of growing from the bottom and creating a leaf array containing most of their biomass near the illuminated surface. Such stands are ultimately limited in biomass partly by turbidity, but mainly by self-shading. Their depth limits, as defined by the deepest water in which they are rooted, are probably fixed by their capacity to grow from reserves, out of the dark bottom waters and into the light before other plants shade them. Size of storage organs is therefore important. These principles apply also to still water conditions.

In many flowing water situations, the occurrence of spates or freshlets following heavy rains severely limits the abundance of submersed species due to strong currents. For example, Bilby (1977) quantified the effects of macrophyte distribution in a stream pool before and after a spate resulting from a large rainstorm in New York. The two dominant species, Elodea canadensis and Potamogeton crispus underwent a pattern of displacement toward lower current speeds following the spate. Most of the reduction in macrophyte cover was where current speeds were highest.

Where current movement is slow as in irrigation canals, submersed plants may become exceedingly abundant, as in south Florida (Blackburn et al., 1968). Likewise, the steady flow and transparent waters of Florida spring runs often support high biomass of submersed species, whose year-round productivity is limited by light (Odum, 1956). In these latter two examples water current serves as an important auxiliary energy source by increasing nutrient availability and exporting waste products. Within a range of slow currents for which flow is laminar (0.02 - 0.5 cm/sec), Westlake (1967) demonstrated that photosynthesis of submersed plants in the laboratory increased with increasing current velocity. However, the high velocities that occur during flooding of most streams and rivers would represent stressful and often quite damaging conditions for macrophytes (Haslam, 1978).

SUSPENDED SEDIMENTS AND THEIR EFFECTS ON SUBMERSED PLANTS

Suspended sediments have effects on submersed macrophytes in addition to those directly related to a reduction in available light. For example, the

composition of bottom materials in which plants are rooted depends on the balance between the rate of sediment supply and the rate at which sediments are carried away by currents. Current velocity, particle density, and particle size are mainly responsible for this balance. These variables will be treated briefly prior to discussing the relationship between macrophytes and sediment types.

The settling velocity of particles is classically described by Stokes law which is formalized as

$$v = \frac{2}{9} \frac{d_1 - d_2}{n} g r^2$$

where v is the velocity of the particle (cm/sec), r is its radius (cm), g is acceleration of gravity, n is the viscosity of the fluid (poises), and d_1 and d_2 are the densities of the particle and fluid (g/cm^3), respectively. If all other conditions are constant, then the settling velocity is directly proportional to the square of the particle radius, and the equation simplifies to $v = C_1 r^2$, where C_1 represents the various constants. This law does not hold for large particles because above about 0.1 mm in diameter the settling velocities are proportional to the square root of the radius according to the impact law. The simplified form of the impact law is $v = C_2 \sqrt{r}$ where various constants are included in C_2 . Viscous forces operable in Stokes law become negligible. Thus the settling velocity will follow the experimental curve shown in Figure 1.

In streams and lakes which have turbulent flow, particles are kept in suspension by kinetic energy that overcomes the gravitational and cohesive forces. The relationship between velocity, particle size and the fate of the particles is shown by the Hj lstrom scheme in Figure 2. This graph incorporates the critical erosion velocity in addition to the settling velocity which brackets the regions in which particles will be eroded, transported, or deposited. This conceptual model is based on a number of assumptions, few of which have much applicability to field situations where the flow velocity is stochastic and particles are seldom spherical, of homogeneous size, or of similar density.

Nevertheless, Figure 2 correctly conveys the concept of segregation of particle size with respect to flow velocity. In considering dredging activities, fine particles with their slow settling velocities will remain in suspension longer and will tend to be transported greater distances than larger particles. Particles from sediments largely composed of organic matter have lower densities and will have an even greater tendency to remain in suspension. It becomes obvious that the duration of shading and the extinction coefficient of the water will depend greatly on the composition of the material brought into suspension, whether by natural (floods) or by human activity (dredging or other disturbances).

Submersed macrophytes and other structural features may act as sediment traps because of their effectiveness in reducing flow velocity. Growth of

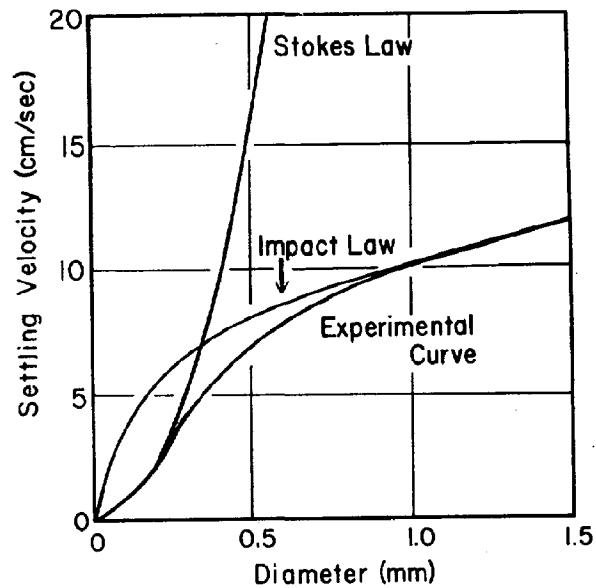


Figure 1. Comparison of settling velocities described by Stokes law and the impact law. The experimental curve is also shown. From STRATIGRAPHY AND SEDIMENTATION, Second Edition, by W.C. Krumbein and L.L. Sloss. W.H. Freeman and Company. Copyright 1963.

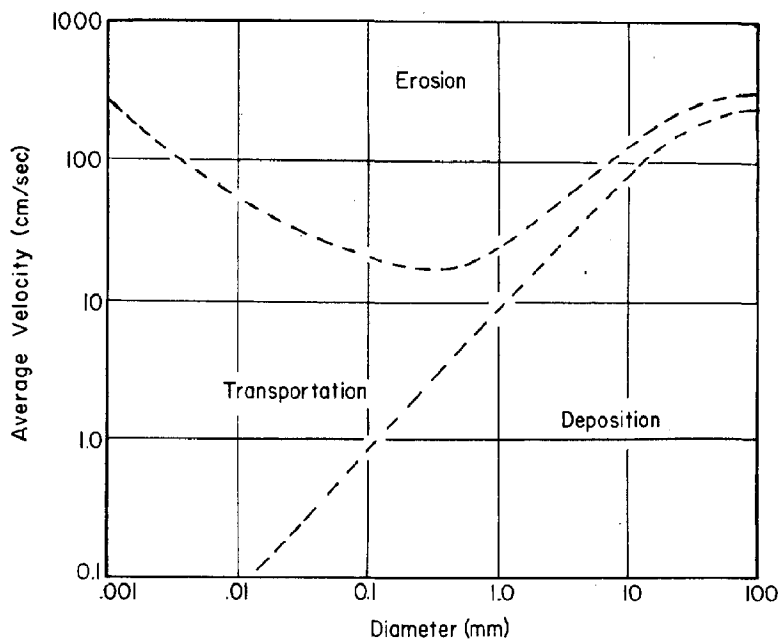


Figure 2. The relationship between current velocity and particle size which determines whether particles will be eroded, transported, or deposited (after Hjulstrom, 1935).

rhizomes and roots in the sediment further stabilizes the substratum. The restriction of vascular plant beds to the relatively low energy sectors of streams contributes to the extremely patchy distribution that is often observed.

In highly organic bottoms, such as in open water areas of peat bogs, the soft ooze severely restricts the establishment of aquatic macrophytes. Plant beds are often restricted to species that produce dense and persistent networks of rhizomes, as in the case of members of the Nymphaeaceae. Although this family is characterized by floating leaves, some members have submersed "water leaves" which may persist year round in the southeastern United States (Brinson and Davis, 1976). The importance of these leaves to the carbon balance of the plant has never been established.

Not only must sediments be stable for successful colonization of macrophytes, but the particle size distribution also influences the species that occur. Spence (1964) showed that in Scottish lochs submersed broad leaf forms predominated in water greater than 150 cm deep only when the sediments were composed of fine muds. However, other factors such as light and turbulence all change with depth, so it is not possible to single out substrate type as the most important variable except perhaps by controlled experiments (Pond, 1903; Brown, 1913; Bourn, 1932; Misra, 1938).

Pearsall's (1920) work on the English lakes during the early part of this century singled out the physicochemical nature of the sediment as the main factor in determining composition of the vegetation, although the original interpretation of these results is somewhat questionable (Spence, 1967). Isoetes was restricted to stony areas with thin silt. This genus apparently cannot colonize areas of sediment deposition because it cannot alter its root level. Potamogeton perfoliatus grows in areas with a high clay fraction, which may also be related to nutrient availability, rather than texture alone. However, life forms with a stoloniferous habit are probably able to adjust to changes in sediment depth except in the most extreme cases of accumulation.

Another aspect of siltation is the accumulation of material on leaf surfaces which reduces light transmission to photosynthetic surfaces and possibly alters gas and nutrient exchange. Sculthorpe (1967) suggested that the linear leaves of Potamogeton pectinatus remain free of settling particles and thus the species may colonize areas unsuited for submersed plants with leaf forms more amenable to silt accumulation. Schiemer and Prosser (1976) confirmed that the sediment coating on Myriophyllum spicatum, which has finely divided, feathery leaves, is markedly greater than for P. pectinatus in sheltered bays of Neusiedlersee, Austria. In addition, they suggested that silt deposition is enhanced by the presence of epiphytic algae on heavily infested macrophytes. Increased plant weight due to silt deposition was also noted as having an inhibitory effect on macrophyte growth. These factors in addition to wave action appear to be largely responsible for the distribution of M. spicatum in Neusiedlersee.

GROWING SEASON AND DORMANCY

Submersed macrophytes may resist the effects of freezing by colonizing depths below the zone of surface ice formation as compared with emergent or floating leaved species that are exposed to freezing temperatures. In spite of this, many temperate submersed species undergo a period of dormancy during the winter and a few species are anatomically and physiologically adapted to overwintering. However, a number of submersed perennials merely subsist with reduced or negligible growth rates and reduced biomass until more favorable light and temperature conditions at the onset of the growing season. Except in cases of a limited number of annuals where viable seed development and favorable conditions for germination must occur, most submersed species are perennial and overwinter by means of vegetative structures.

Weber and Nooden (1976a, b) described the role of turions in the overwintering of Myriophyllum verticillatum. In this species turions are specialized compact buds that develop from nodes late in the growing season as a response to photoperiod and possibly temperature. These reproductive structures sink to the bottom after detachment from the parent plant. Dormancy is broken by cold temperatures (0 - 4° C) which compares well with observed turion germination before ice breakup.

Apart from highly modified organs such as turions, many other less specialized organs appear equally capable of overwintering. These include dormant apices and offsets, root tubers, stolons, and rhizomes. Dormant apices and offsets as well as turions can be important in plant dispersal. These structures in submersed aquatic plants appear to substitute for seed dispersal more commonly found in emergent or floating leaved species.

In addition to lower water temperatures and reduced day length during the nongrowing season, the presence of an ice and snow cover in northern latitudes poses severe restrictions on light penetration. Species that may have only reduced biomass and growth during the winter season if open water persists will be much reduced in more northern waters that become completely iced in. This may result in regional differences in standing crops of submersed plants at the beginning of the growing season.

The presence of ice may also result in physical disruption of macrophyte communities. Martin and Uhler (1939) described the scouring action of ice masses during spring breakup in flowing waters and shallow lentic habitats that may cause severe damage to beds of submersed plants.

NUTRIENT AVAILABILITY AND UPTAKE

There has been considerable controversy concerning the importance of roots in nutrient uptake from sediments. It is clear from a number of studies that roots do accumulate nutrients from the sediments and these may be translocated to the shoots. However, in many aquatic plants, significant ion absorption occurs by leaves and there appears to be a great diversity in the relative importance of roots and shoots in mineral nutrition.

Figure 3 illustrates the spectrum of all possible cases for aquatic macrophytes in which the x-axis represents a gradient in life form, root-shoot ratio, or anatomical complexity (Denny, 1972). Emergent species will obtain most of their mineral nutrition from the sediments, while those that have floating leaves are intermediate between emergent and submersed plants.

The actual amount of nutrient absorption in field situations may be related also to the relative supply in the water and the sediments. For example, Bole and Allan (1978) demonstrated that Myriophyllum spicatum and Hydrilla verticillata utilized phosphorus from the sediment until concentrations in the water reach a threshold value which differs for the two species. Above these water concentrations uptake from the water column increases. Nutrient availability is not based solely on concentration since flowing waters of low concentration may actually be a better source of nutrients than higher concentrations in quiescent waters. Dense growths of submersed communities often require nitrogen and phosphorus in excess of the amount present in the water at any one time. Sediment texture and cation exchange capacity may also be important in the nutrient supply to roots. Since it has been demonstrated that some aquatic macrophytes translocate phosphorus (Twilley et al., 1977) and nitrogen (Nichols and Keeney, 1976) both from roots to shoots and from shoots to roots, it is unlikely that the sediments or the water alone are the singular source of nutrients.

Although nitrogen and phosphorus are generally believed to be the most important limiting nutrients in fresh waters, there are no clear cut cases where submersed macrophytes are excluded by the paucity of either. Rather it would seem that the rate of productivity may be limited by the supply of these nutrients. However, in the case of soft and hard waters (low and high CaCO_3 concentration, respectively) there appears to be an important dichotomy in species distribution. This has been reviewed extensively by Hutchinson (1975) who also noted that pH may play an important role in species distribution in soft waters.

BIOLOGICAL FACTORS

The absence of submersed aquatic plants in fertile lakes and ponds has often been attributed to shading by dense populations of phytoplankton. Jupp and Spence (1977a) reported an inverse correlation between biomass of Potamogeton filiformis and open water chlorophyll *a* concentrations at certain times during a three-year study of Loch Leven, Scotland. Scums of blue-green algae accumulating near the shore during Anabaena flos-aquae blooms intensified shading in macrophyte beds. Jupp and Spence suggested that these algal blooms, apparently enhanced by high levels of phosphorus from cultural eutrophication, retard macrophyte growth by shading and possibly by producing elevated pH conditions.

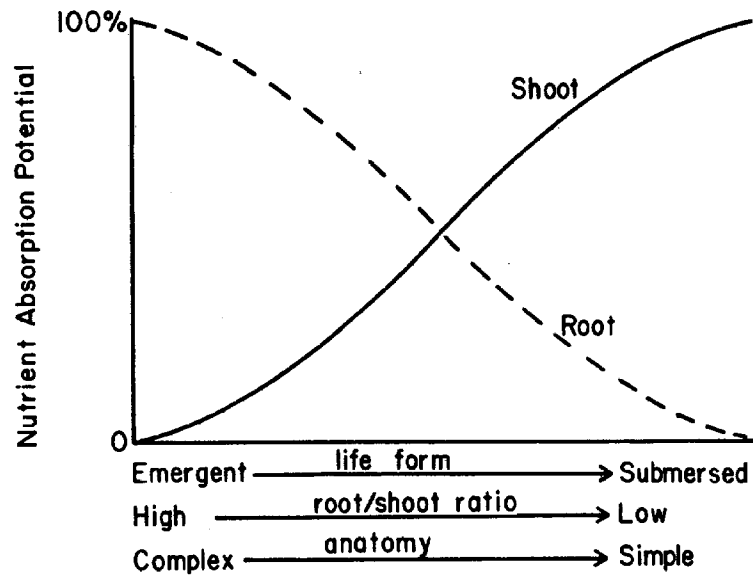


Figure 3. Schematic diagram of factors that contribute towards a tendency for nutrient absorption by roots or shoots. Axes are arbitrary. Modified from Denny (1972).

However, Phillips et al. (1978) set forth a convincing argument for the role of epiphytes and filamentous algae in suppressing submersed macrophyte growth due to shading. They suggest that dense phytoplankton develops subsequently to the macrophyte decline rather than being its cause. Although the effects of shading will be treated more fully in later sections, the scheme of Wetzel and Hough (1973) in the succession of littoral communities with increasing fertility (Figure 4) is of interest here. According to this, nutrients are initially limiting to macrophyte productivity and growth is proportional to nutrient availability. At high concentrations of nutrients, submersed macrophytes will be excluded due to shading by phytoplankton, epiphytes, and filamentous algae. The model probably applies somewhat to flowing water situations although phytoplankton is expected to be less important and physical factors more important than in lakes.

The importance of grazing on submersed plants has never received a comprehensive review. Repeated mowings during a single growing season may in some ways simulate high grazing intensities (Davis, in preparation). However, when one considers the total effect of consumer activity, the disruptive activity of feeding, whether on macrophytes or other food sources, may be quite substantial. For example, the feeding activities of carp in Lake Mattamuskeet, North Carolina, increased turbidity so greatly that submersed waterfowl food plants did not become established until the fish were removed (Cahoon, 1953).

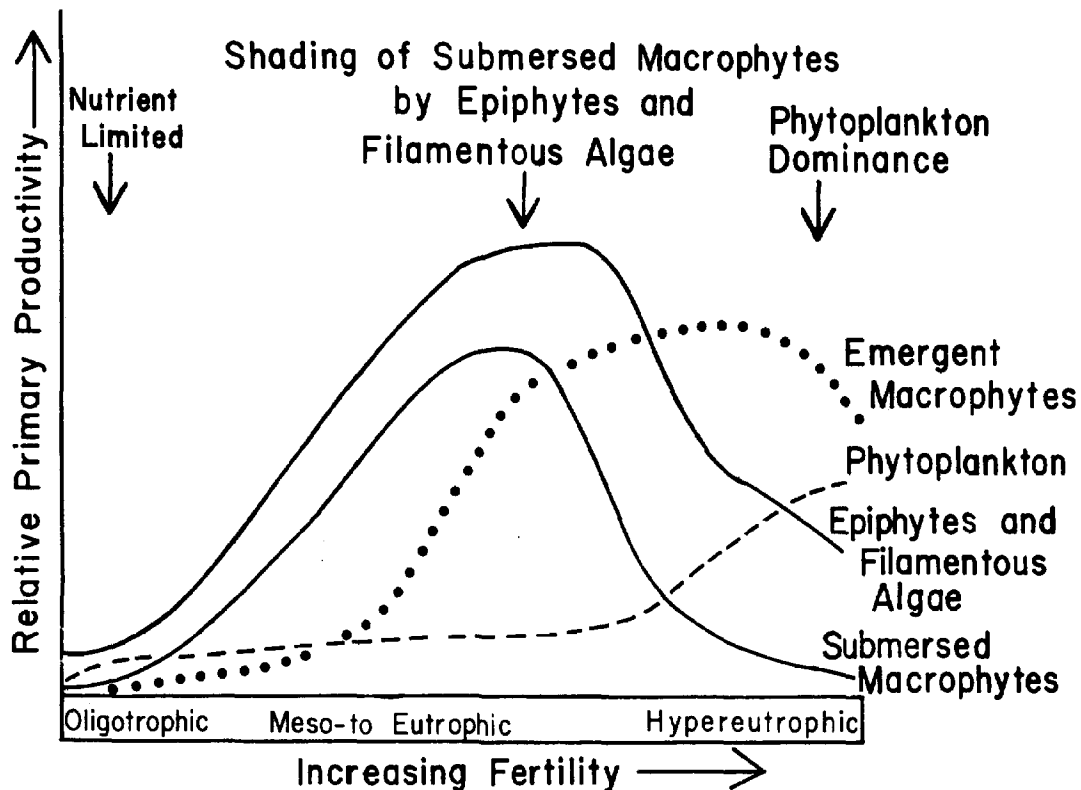


Figure 4. Hypothetical changes in relative primary productivity of submersed, emergent, epiphytic, and planktonic communities with increasing nutrient enrichment (after Hough and Wetzel, 1973, with modifications according to Phillips et al., 1978).

Many migratory waterfowl species are primary consumers and may have temporarily devastating effects on wetlands, particularly marshes that receive overgrazing by geese (Lynch, et al., 1947). Muskrat "eat outs" have also been observed, but again it is the conspicuous emergent species studied that are reported to have heavy damage. Anderson and Low (1976) studied grazing rates on *Potamogeton pectinatus* by ducks in the open water region of a Mantioba prairie marsh. By comparing biomass in enclosures and in areas not excluding birds, they estimated that 40 percent of the peak standing crop of foliage and 18 percent of the peak standing crop of tubers were removed. Some of this reduced biomass was not consumed but was lost by activities associated with feeding. By comparison, Jupp and Spence (1977b) calculated that 30 percent of the peak standing crop of *P. filiformis* was removed by waterfowl grazing in Loch Leven. In this case, only shoot biomass showed significant grazing losses, perhaps due to difficulty of uprooting tubers in the fine clay substrate.

HYDROSTATIC PRESSURE

In exceptionally clear lakes of great depth, it would appear that there is adequate light for macrophyte growth at depths beyond the observed plant

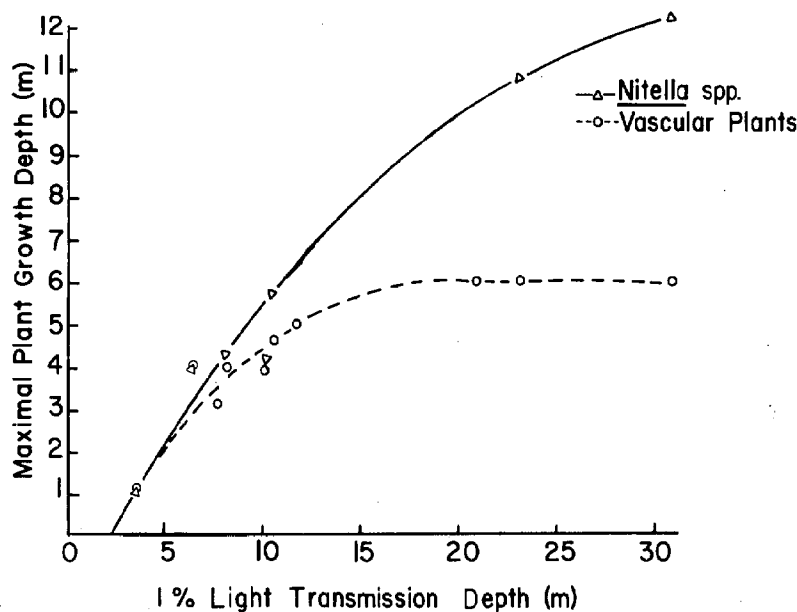


Figure 5. Depth maxima for aquatic vascular plants and *Nitella* spp. as related to the 1 percent light transmission depth for some British lakes (data from Spence, 1976).

distribution. At lower altitudes one atmosphere of excess pressure is equal to the pressure in about 10 m of water. Hence, depth maxima of species tolerant to low light levels suggest that hydrostatic pressure is a factor in depth limitation of plant presence. As reviewed by Hutchinson (1975), charophytes, mosses, and the lower vascular plants tend to grow at greater depths than submersed angiosperms. R. G. Wetzel (quoted in Hutchinson, 1975) found that 0.5 atmosphere of excess pressure reduced photosynthesis in *Najas flexilis* by 50 percent. Spence (1976) compared depth maxima of vascular plants (including lower vascular plants) with various nonvascular plants in 23 freshwater lakes. Depth maxima summarized by Spence for submersed vascular plants and the non-vascular charophyte, *Nitella* spp., in some British lakes are plotted against the depth of 1 percent light transmission for each lake (Figure 5). Only the data collected by divers (as compared with from a boat) are used. The depth maxima for the vascular plants plateau at around 5.5 to 6 m regardless of water transparency. This suggests that factors other than available light limited the depth maxima for vascular plants and a case for hydrostatic pressure effects is strongly suggested. Depth maxima for *Nitella* spp., on the other hand, increased throughout the range with increasing light penetration, suggesting light limitation as being of primary importance.

Adaptations which result in resistance to hydrostatic pressure are unclear. In laboratory experiments physiological and/or anatomical and growth changes in submersed angiosperms become apparent when hydrostatic pressures of 0.5 to 1 atmosphere excess are applied (Gessner, 1952; Ferling, 1957). One response is a decrease in the size of intercellular air spaces. Of course, environmental factors such as sediment characteristics, nutrient distribution, dissolved oxygen, temperature, and the quality of light reaching the bottom may play a part in restricting depth penetration by plants.

RESPONSES OF SUBMERSED PLANTS TO LIGHT AND TURBIDITY

LIGHT ATTENUATION

The depth to which submersed aquatic vascular plants are distributed depends on the availability of light, if no other factors such as hydrostatic pressure, nutrient supply, substrate composition, and turbulence limit growth. Three factors affect light attenuation: absorption by water itself, absorption by suspended particles, and absorption by dissolved substances.

Monochromatic light passing through chemically pure water is absorbed exponentially and thus decreases at a constant rate with increasing increments of depth. This relationship can be expressed as the extinction coefficient, η , which decreases from the red to the blue end of the visible spectrum. The extinction coefficient, η , is a function of the light intensity at the surface (I_0) and the intensity at depth z in meters

$$\eta = \frac{\ln I_0 - \ln I_z}{z}$$

The extinction coefficients of natural waters deviate greatly from those of pure water due to the presence of dissolved and particulate substances which absorb and scatter light. The spectral quality of light is particularly affected by dissolved substances, since light scattering by particulate matter is relatively nonspecific in optical effects.

The extinction coefficient of natural waters is separated into three components such that

$$\eta_t = \eta_w + \eta_p + \eta_c$$

where η_t is the total extinction coefficient, and the remaining terms are due to water, suspended particulates, and dissolved color, respectively. Thus the expression can be rearranged so that the intensity of light, I_z , at a depth of one meter below I_0 is

$$I_z = I_0 e^{-\eta_w} \times e^{-\eta_p} \times e^{-\eta_c}$$

Figure 6, adapted from the data of James and Birge (1938) for Lake George in Wisconsin, clearly shows the effects of absorption by each of these components. (The data are graphed as percentile absorption, expressed by the formula, $100 (I_0 - I_z)I_0$, where I_z is at 1 m depth.) Short wavelengths (violet and blue) are most strongly absorbed by the dissolved material which mostly consists of dissolved organic compounds, absorption of long wavelengths (red and infrared) is due mostly to water, while the particulate matter is quite nonspecific in its absorption properties, at least when in low concentration. However, in using sediment concentrations between 50 and 5,000 ppm, Otto and Enger (1960) found that the red wavelengths penetrated somewhat further than blue. The spectral discrimination was greater for a commercial sodium base montmorillonite type bentonite than for a sediment obtained from a reservoir. This indicates that although suspended sediments may have a negligible effect on spectral quality at low concentrations (< 50 ppm), higher concentrations may cause significant shifts in the relative penetration of various wavelengths. Selective absorption by algal pigments may occur in the blue (400-500 nm) and red (640-680 nm) when phytoplankton are dense, but the amount is minor when compared with the attenuation by particulate matter throughout the visible spectrum (Westlake, 1966).

Vertical extinction coefficients then represent a composite of all wavelengths and vary considerably among natural waters depending on the contribution by suspended particulate and dissolved components. Values of η_t range from about 0.2 for exceptionally clear lakes such as Lake Tahoe, California, to values in excess of 10 where turbidity is extremely high such as for reservoirs receiving inputs from flooding rivers (Wetzel, 1975; Westlake, 1966). Ice cover reduces light transmission to variable degrees depending on whether the ice is clear, contains bubbles, or is stained. Theoretically, clear ice transmits light better than natural water because the dissolved substances have been reduced. However, snow cover reduces transmission considerably. Self shading by submerged macrophytes may be large depending on biomass, and as little as 0.1 percent of the surface light may reach the bottom of a river weed bed, mostly in the green wavebands (Westlake, 1966).

RELATIONSHIP OF ACTUAL LIGHT TRANSMISSION AND SECCHI DISC TRANSPARENCY ESTIMATES TO THE EUPHOTIC ZONE

The euphotic zone is the region from the surface to the depth at which 99 percent of the incident surface light has disappeared. Work based on response of phytoplankton suggests that the intensity of light at this level, i.e., 1 percent of the surface light, represents the compensation light intensity at which photosynthesis and plant respiration are in balance. For many of the studies we cite, only Secchi disc transparency depths are available. It would be valuable to be able to relate the Secchi depth to the more

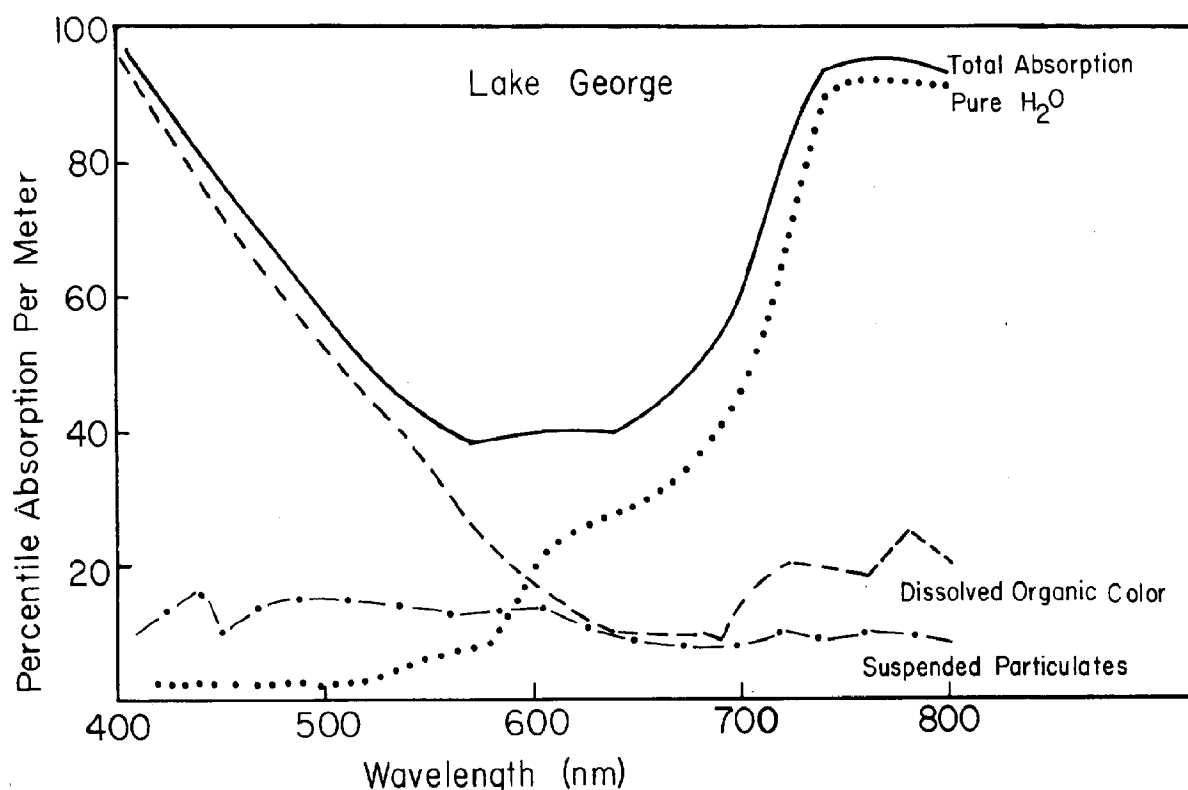


Figure 6. Total absorption spectrum of water from Lake George, Wisconsin, as compared with spectra for pure water, dissolved organic color, and suspended particulates. Modified from James and Birge (1938).

theoretically sound measurements of extinction coefficient or percent light penetration at which the Secchi disc disappears. Attempts have been made to do this (Poole and Atkins, 1929; Verduin, 1956; Cole and Barry, 1973). As Hutchinson (1957) pointed out, the Secchi depth measurement actually is based on a comparison of the brightness of the disc and the water surrounding it. Thus light reflected from the bottom in shallow water or scattered upward by silt-laden waters can introduce considerable error. Nevertheless, factors of 2.7 to 3.0 times the Secchi depth have been found to approximate the 1 percent level in many cases (Cole, 1975). Based on empirical evidence for coastal waters, Holmes (1970) suggested that a factor of 3.5 might be most appropriate in water with a Secchi depth of less than 5 m and a factor of 2.0 for water with a Secchi depth between 5 and 12 m. However, as will be discussed later, lower factors appear to be more appropriate for relatively clear waters.

Within a single lake, seston would be expected to have a greater correlation with Secchi depth transparency than dissolved colored compounds because of greater seasonal change in suspended material. However, between lakes, the confounding effects of varying color would weaken the relationship between Secchi depths and extinction coefficients.

DEPTH ZONATION AND TURBIDITY TOLERANCE OF SUBMERSED SPECIES

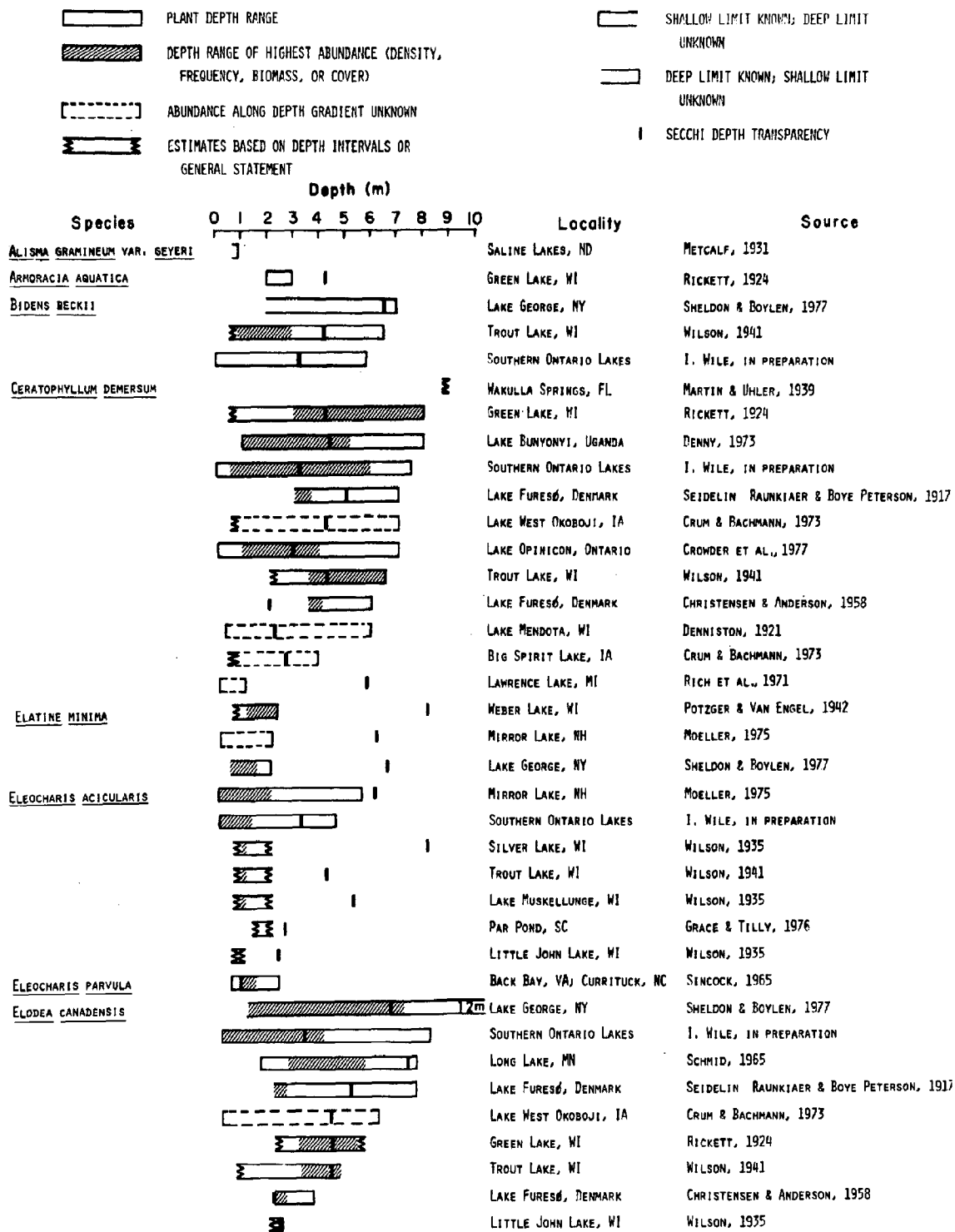
Species that become established and grow in the deeper regions of aquatic ecosystems where only a small fraction of the surface irradiation remains are better adapted to survival at low levels of light than those restricted to shallower and better illuminated zones. In shallow aquatic ecosystems where light is rapidly attenuated by high concentrations of suspended sediments, the same species tolerant to low levels of light might be expected to compete more effectively than those requiring high light intensities. To test this hypothesis, the depth distributions for a number of species from diverse systems are presented graphically with their Secchi depth estimates in Figure 7. Available North American depth distribution records of submersed angiosperms have been tabulated for aquatic systems where water depths were such that the maximum depth of submersed plants would likely be limited by irradiance rather than the shallowness of the system. Some data are given for areas other than North America but an extensive search of world literature was not made.

The variety of methods of collecting and reporting the data summarized in Figure 7 and the complexity and variations within and between the ecosystems put the comparative analyses to be made later within the realm of approximations. Normally for each species the shallowest and greatest depths reported are shown along the depth axis and the area of greatest frequency, density, cover, or standing crop is indicated by cross-hatching. No absolute values are given; only the relative occurrence of a species along the depth gradient is graphed. These data were often given in the literature just as reported here, but in some cases we have given our best estimate. For example, depth distribution may have been reported within range classes such as percent frequency at 0-1, 1-3 and 3-8 m (Rickett, 1922, 1924; Wilson, 1935, 1941). In this specific case the minimum depth would be graphed as 0.5 m if the species occurred at 0-1 m while the maximum depth would be graphed as 5.5 m if the species occurred at 3-8 m.

Secchi disc depths as given in the literature or as estimated from submarine photometer readings are given when available. There are many problems associated with attempting to relate Secchi readings to the light environment of the plant. These range from the visual acuity of the observer to the necessity of using Secchi data taken at times other than the growing season for the plants in question. One possible source of error in Secchi readings which doesn't appear to be serious is the lack of standardization in disc size and contrast (white as compared with black and white) common in earlier studies. Baker and Magnuson (1976) found no significant differences in transparencies in Crystal Lake, Wisconsin, as measured with a 20 cm black and white disc and a 10 cm white disc.

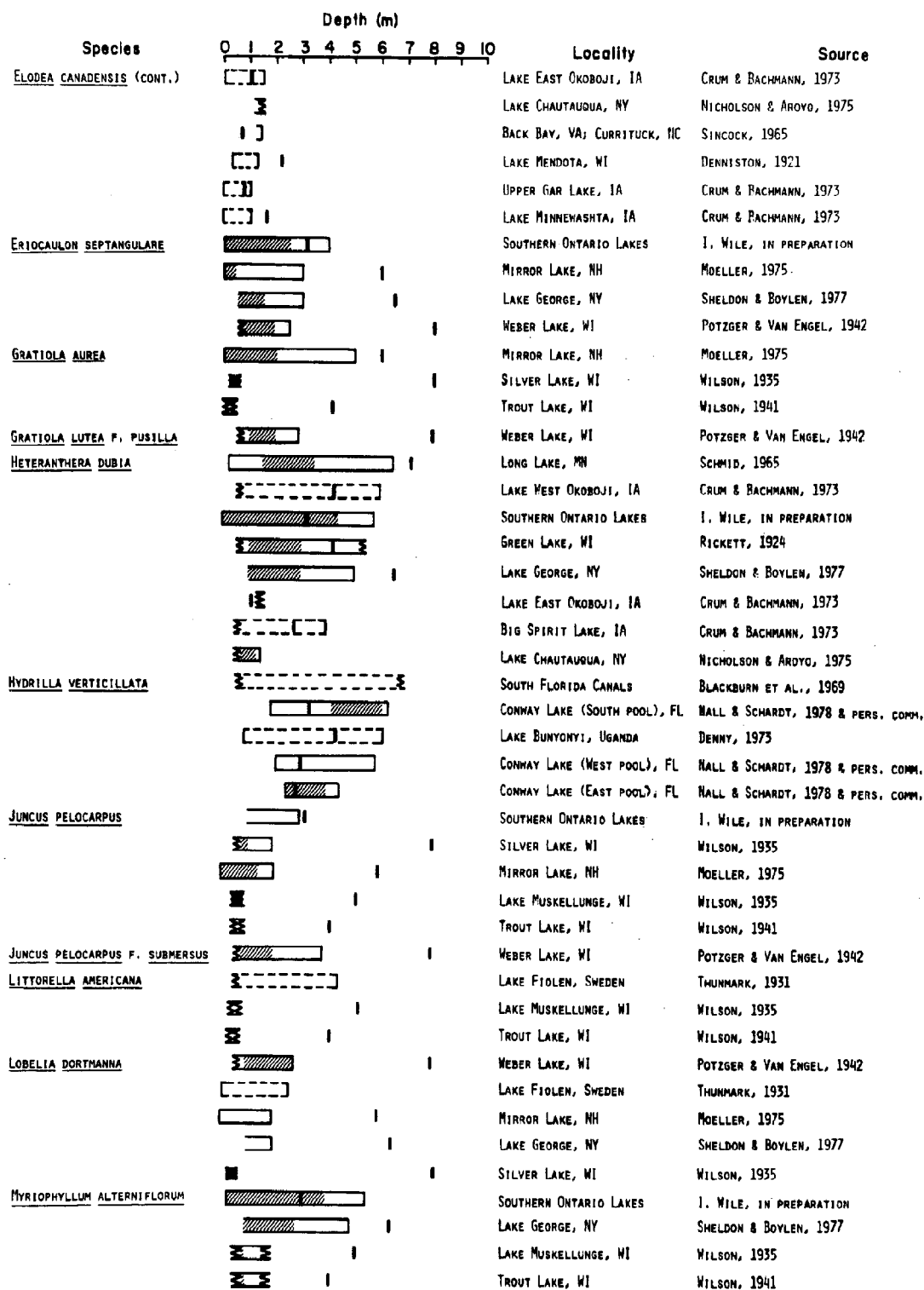
To convert occasional clear water light transmission data taken with a submarine photometer to Secchi depth transparency estimates, the depth (m) at the 1 percent light level was divided by 1.7. This factor is consistent with observations by Wile (in preparation) for fresh waters in southern Canada and

Figure 7. Depth distributions for submersed macrophytes.



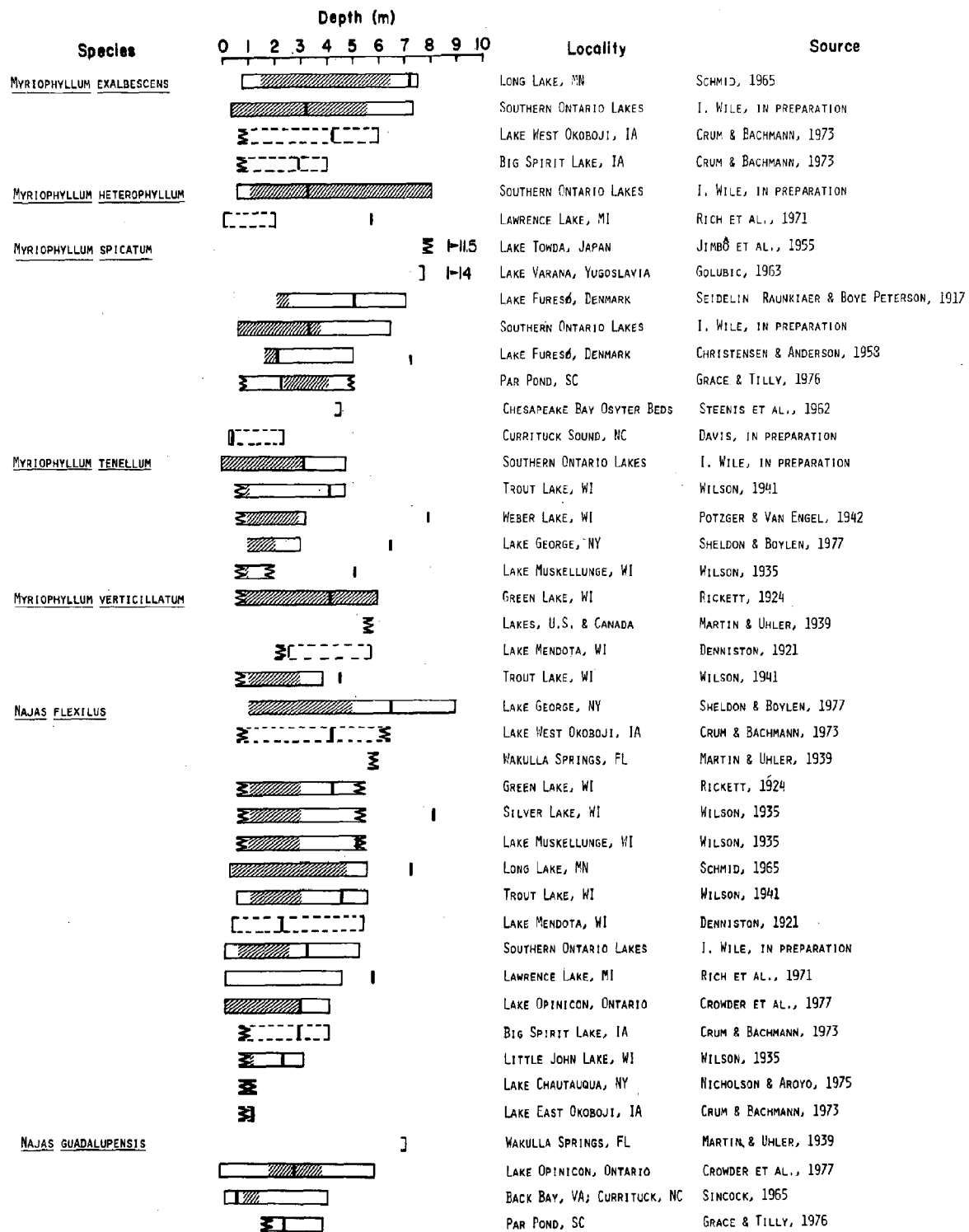
Continued

Figure 7 (Continued)



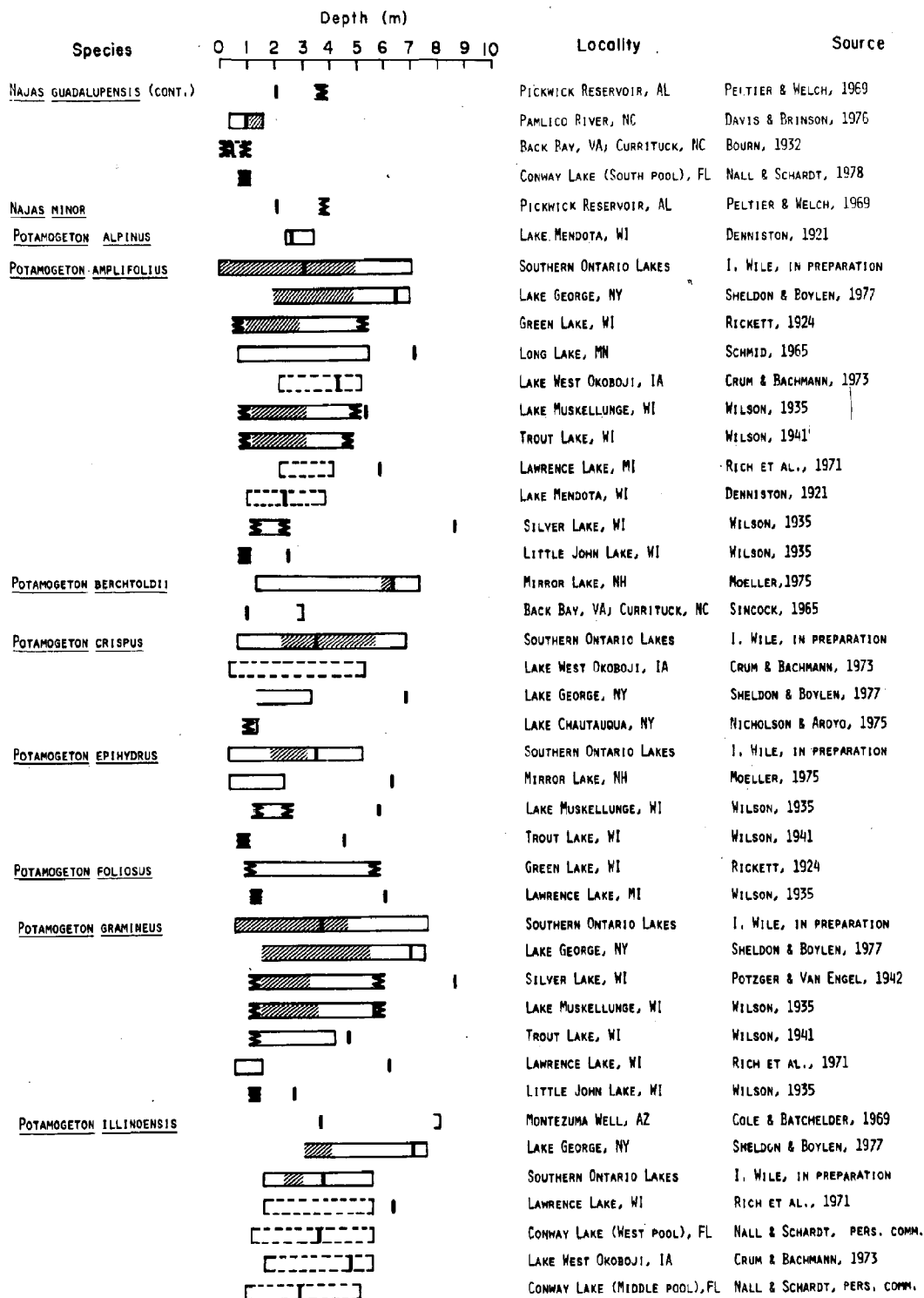
Continued

Figure 7 (Continued)



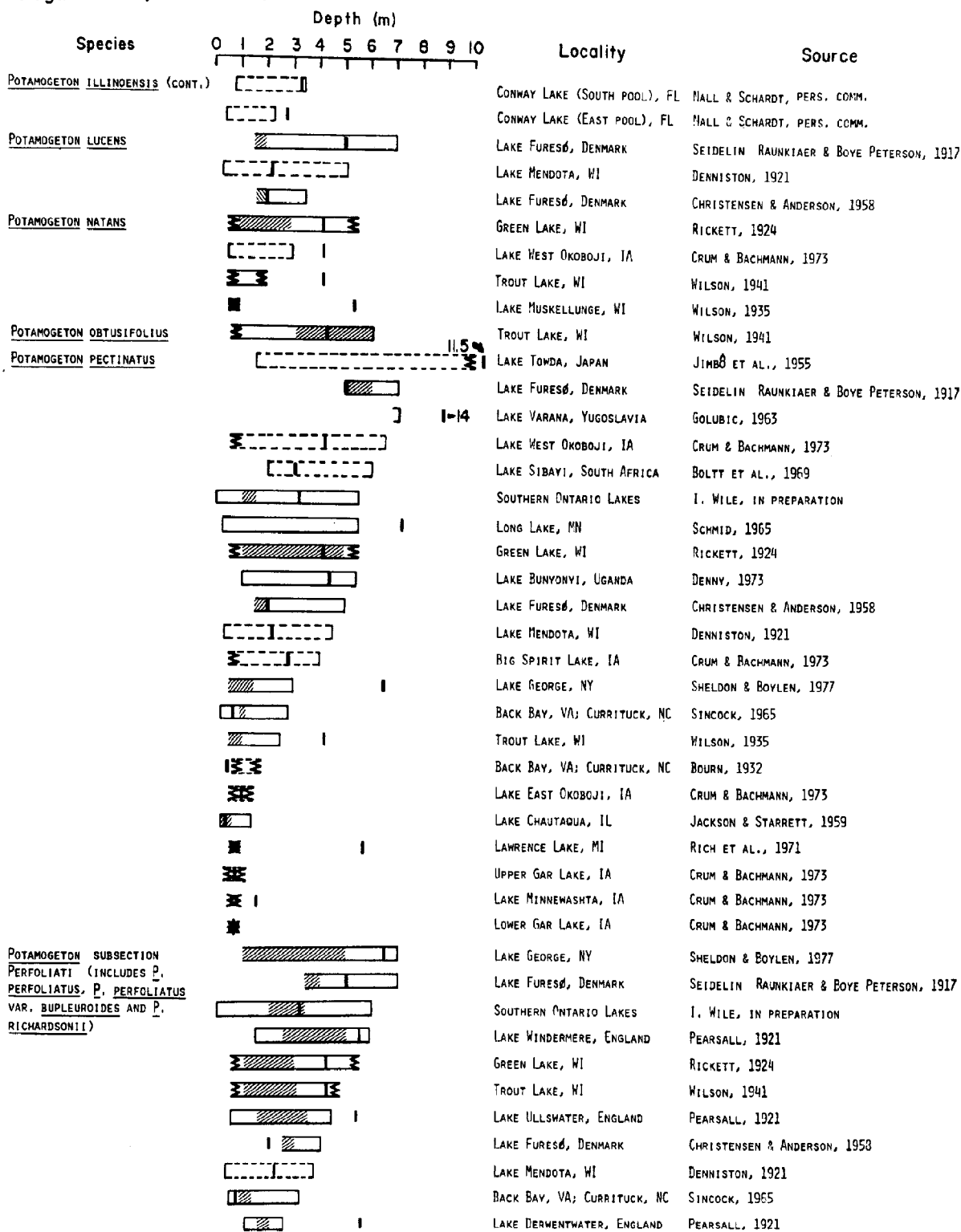
Continued

Figure 7 (Continued)



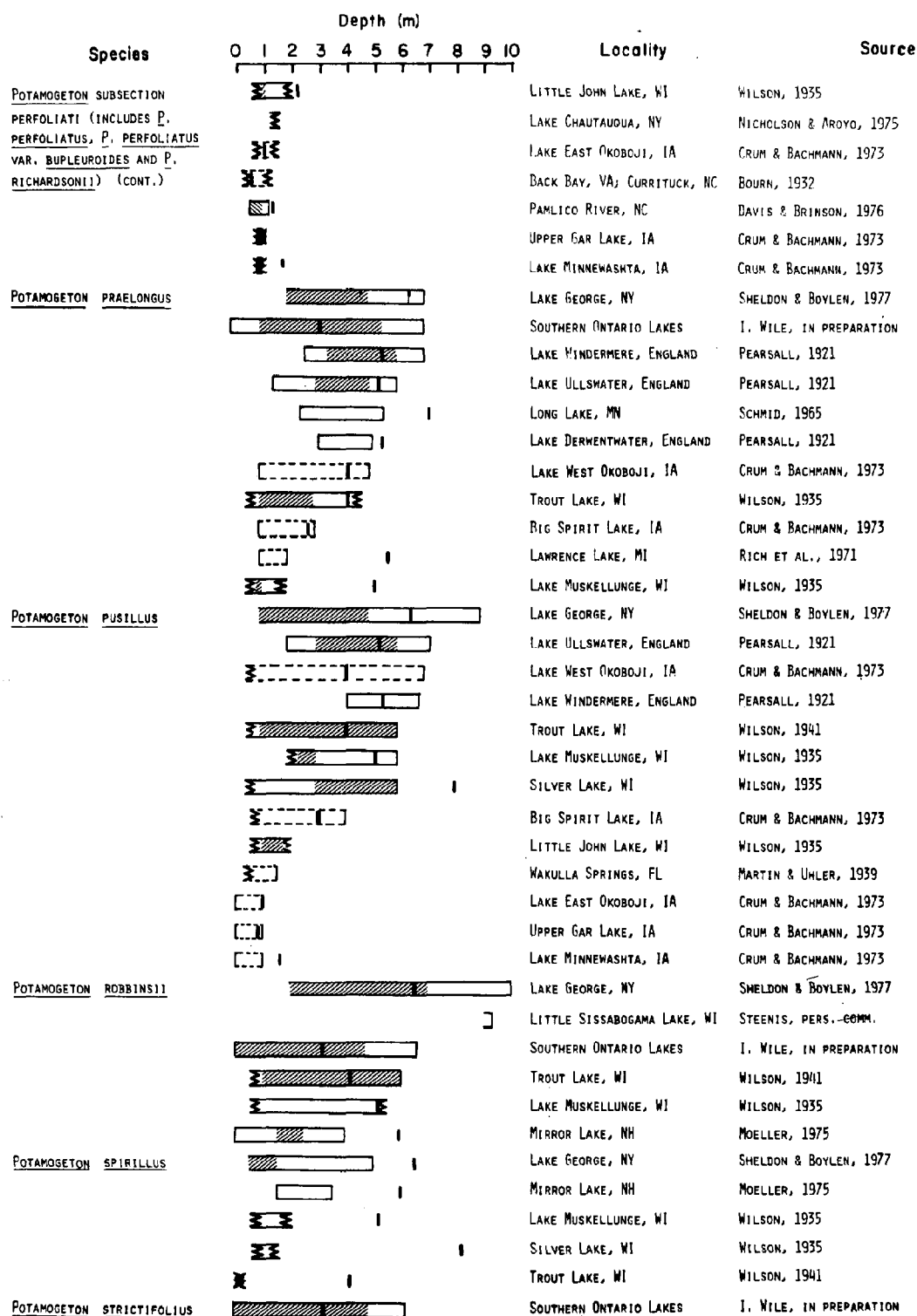
Continued

Figure 7 (Continued)



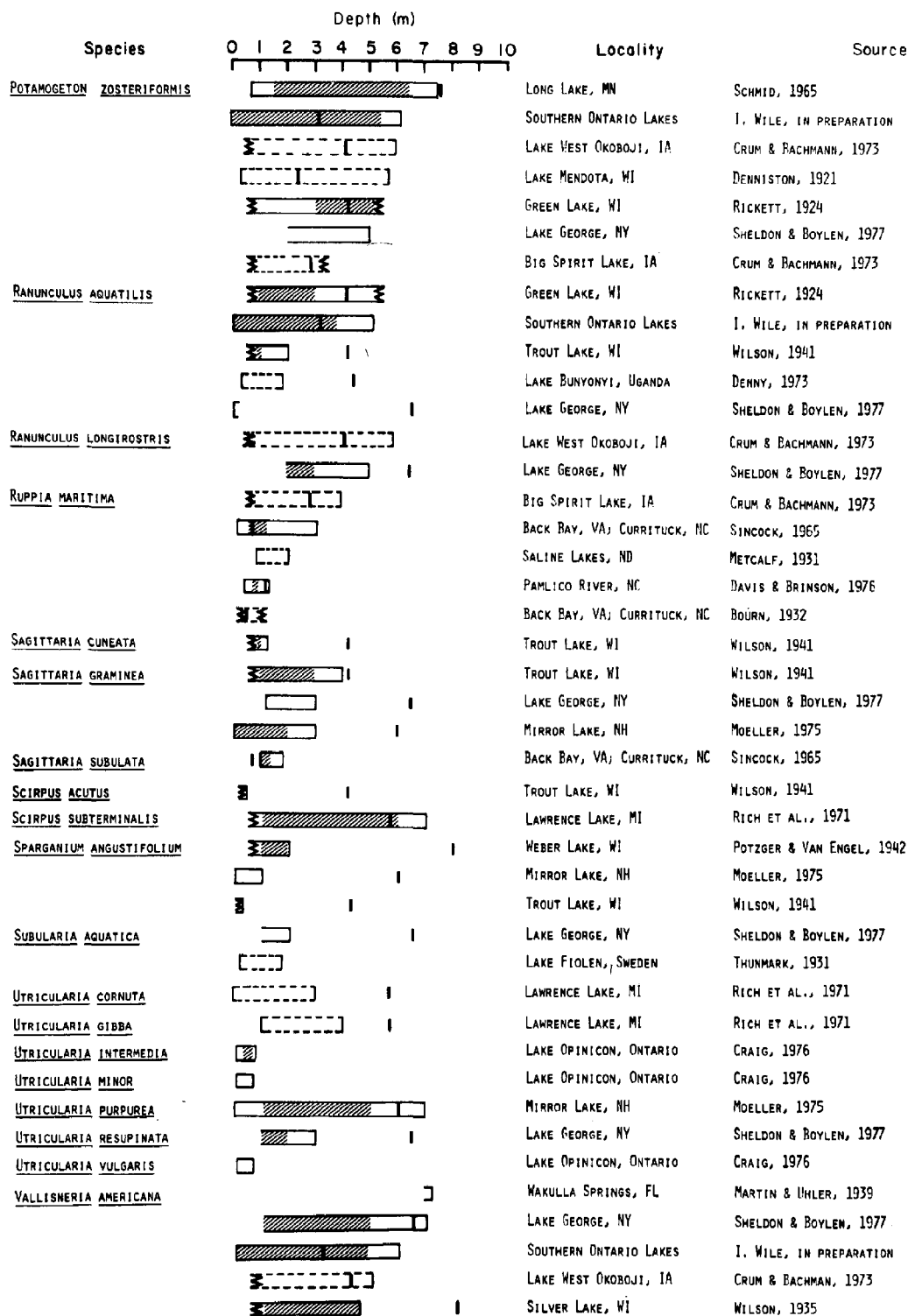
Continued

Figure 7 (Continued)



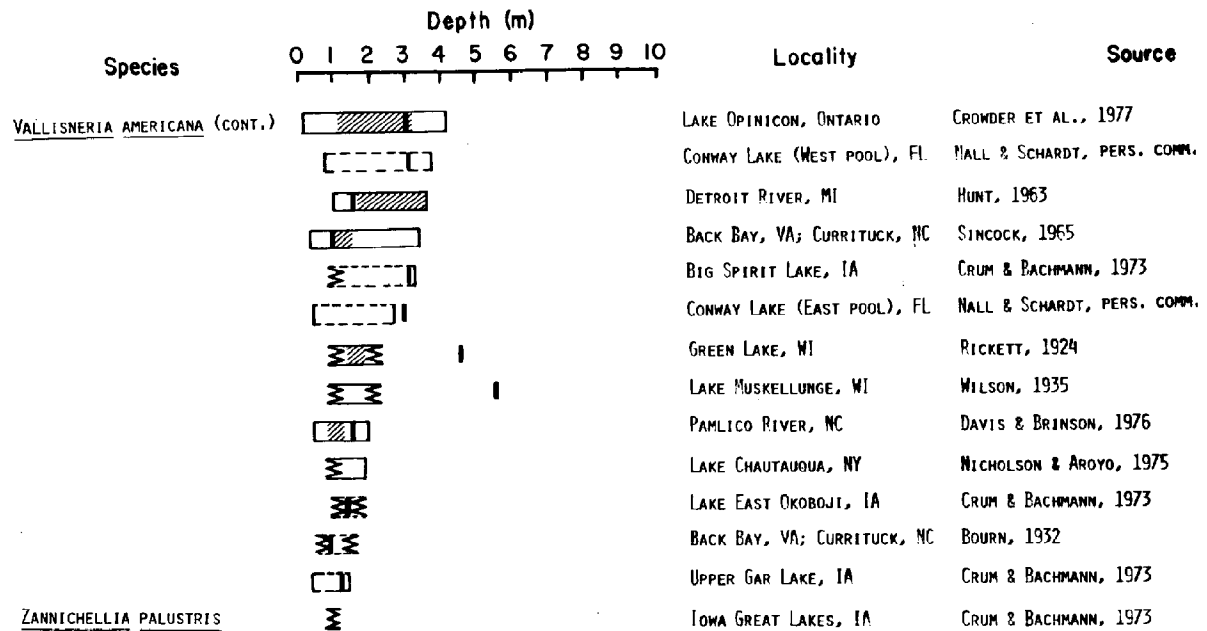
Continued

Figure 7 (Continued)



Continued

Figure 7 (Concluded)



Wetzel (1975; Figures 5-9 and 5-16) for Lawrence Lake, Michigan. Based on studies of turbid waters in Back Bay, Virginia (Sincock, 1965), a conversion factor of 2.5 was used for the data of Bourn (1932).

Perhaps the maximum depths of plant growth recorded in Figure 7 are more reliable than other information given. However, as discussed by Hutchinson (1975) and Spence (1976), there can be problems in establishing the maximum depth in a water body where a species is rooted and growing. Accuracy includes judgement as to whether a small number of plants (or the plant) at a depth are living and are truly rooted. *Ceratophyllum demersum* is a special problem because it does not form roots although a portion of the shoot often becomes embedded in the sediment and thus "rooted" (Arber, 1920). Other species such as *Myriophyllum spicatum* at times produce rooted floating shoot fragments which normally sink with time. Hence shoots of *C. demersum* and other species may be carried to the deeper areas and sink to the sediment where they may soon become moribund in the more stressful environment. Even though some shoots were found as deep as 9.2 m, Spence (1976) set the macrophyte limit for Loch of Lowes at 3.9 m which was close to the 1 percent cover line of 3.6 m. The increasing use of SCUBA divers in studies of submersed macrophytes should lead to more accurate data.

Though the ecological importance of straggling plants surviving in the lower depths is probably minimal, depth records suggest that there are physiological limits due to hydrostatic pressure as discussed previously. Hutchinson (1975), in summarizing depth records for a number of aquatic macrophytes, rejected some of the published depths of colonization due to problems mentioned above. He suggested that the record depth for submersed

freshwater angiosperms was for Potamogeton strictus Philippi, which is apparently not found in North America (Shetler and Skog, 1978). Tutin (1940) found this species at slightly deeper than 11 m in the high mountain Lake Titicaca, Peru-Bolivia. Recent data, especially those of Moeller (1975), Sheldon and Boylen (1977), and Wile (in preparation), all from the same geographical area of northeastern United States and southeastern Canada, extend the depth ranges for a number of species native to North America. Perhaps the most notable depth record is for Elodea canadensis which was found at one of the 12 m sampling stations in Lake George, New York (Sheldon and Boylen, 1977).

Relationship between Maximum Depth Distribution and Secchi Transparency

Figure 8 is a summary of depth records for 10 species in Figure 7 plotted as a function of Secchi depth. Some trends are discernable and factors which may affect depth distribution will be discussed. However, conclusions drawn from these graphs are necessarily tentative owing to the paucity of data points as well as problems already mentioned in interpretation of the original data. The resistance of these species to environmental changes will be discussed further on page 44.

Since Eleocharis acicularis is a sedge, one might judge a priori that it is a shallow water species. This is confirmed by depth records of 2 m or less for five of the seven data points (Figure 8a). The scattering of the points suggests that E. acicularis does not respond to water clarity in a predictable manner as do some other species that have increasing maximum depth distribution with increasing Secchi depth. In fact, Wilson (1935) placed it in an ecological group of species (mainly rosette) which becomes totally submerged only in response to changing lake conditions. Other species placed in this group were Lobelia dortmanna, Juncus pelocarpus, and Gratiola aurea. These relatively clear water species with generally shallow maximum depth records (Figure 7) are probably limited in depth maxima by factors other than reduced irradiance. An affinity for sandy sediments which are normally characteristic of shallow areas subjected to fetch and water turbulence is one possible explanation for the depth distribution patterns. Laboratory and field experiments have shown that certain species grow best when rooted in specific types of aquasoils (Pond, 1903; Brown, 1913; Bourn, 1932; Misra, 1938).

The relationship between depth maxima and Secchi depths for Potamogeton praelongus (Figure 8b) can be considered representative of several species of this genus with a North American distribution, primarily in clear fresh waters in Canada and northern United States. In addition to P. praelongus these species include P. robbinsii, P. zosteriformis, P. amplifolius, and P. gramineus. Since depth maxima for this group are normally high, one might expect that these species would tend to survive under reduced light penetration due to suspended particles. However, some studies of long term changes in lakes where turbidity has increased show that these northern species tend to disappear or decrease in biomass (Volker and Smith, 1965; Lind and Cottam,

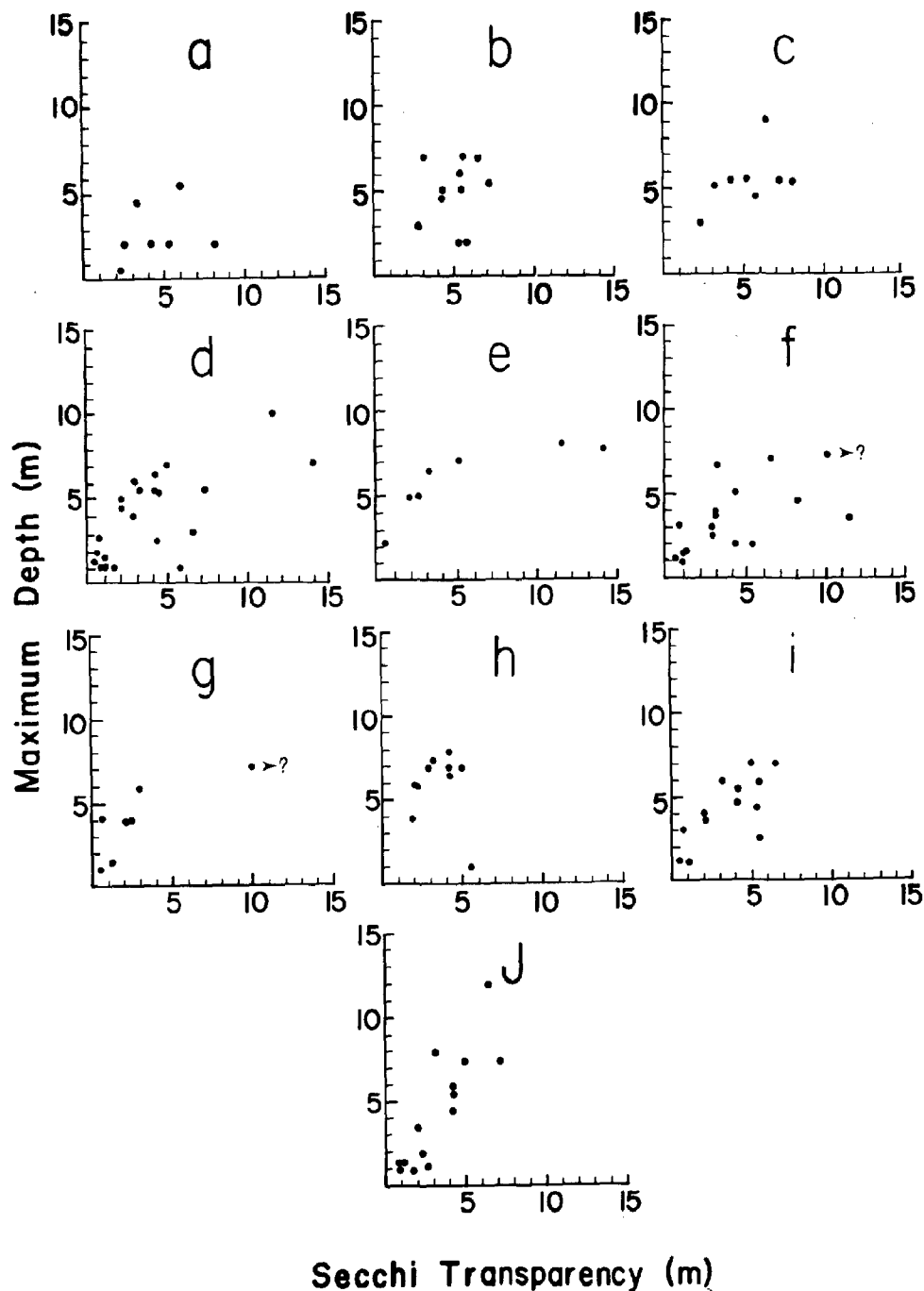


Figure 8. Maximum depth distribution of selected species from Figure 7 plotted against Secchi disc transparencies of the waters where the distributions were observed: (a) *Eleocharis acicularis*, (b) *Potamogeton praelongus*, (c) *Najas flexilis*, (d) *Potamogeton pectinatus*, (e) *Myriophyllum spicatum*, (f) *Vallisneria americana*, (g) *Najas guadalupensis*, (h) *Ceratophyllum demersum*, (i) *Potamogeton* subsection *Perfoliati*, (j) *Elodea canadensis*.

1969; Stuckey, 1971; Nichols and Mori, 1971; Crum and Bachmann, 1973; Baumann et al., 1974; Bumby, 1977). Especially striking was the virtual elimination of the group with increasing human activities over 70 years in the vicinity of Put-In-Bay Harbor, Lake Erie, Ohio (Stuckey, 1971). Though these species do well at the low light intensities of deeper waters, they appear to be restricted to rather narrow conditions which do not include highly turbid waters.

A number of physical and biological changes are likely to be associated with increasing turbidities from increasing suspended sediments. These include increasing inorganic nutrient levels and changes in biological components of the ecosystem. Of 19 lakes and ponds of Southern Ontario studied by McCombie and Wile (1971), Potamogeton amplifolius was present only in the most oligotrophic impoundment. Disappearance or reduced importance of northern species has also been associated with increased importance of other species, especially Myriophyllum spicatum (Lind and Cottam, 1969; Nichols and Mori, 1971; Steenis, 1970) and perhaps P. crispus (Fassett, 1957; Stuckey, 1971; McCombie and Wile, 1971; McIntosh et al., 1978). Both of these species have been naturalized from Europe.

Najas flexilis (Figure 8c) is found under a wider range of Secchi depths than the northern species of Potamogeton. This species principally has a northern distribution and does not range southward sufficiently to be considered cosmopolitan. There does not appear to be much tendency for an increase in maximum depth with increasing water transparency for the data points available.

Compared with the three species just discussed, the remaining species all show some degree of linearity between Secchi transparency and maximum depth distribution (Figures 8d-8j). All except Najas guadalupensis, which tends to have southern affinities, are strongly cosmopolitan. Potamogeton pectinatus grows well under a wide variety of conditions. This is consistent with the wide range of Secchi transparencies and depth records for the plant. In their study of Canadian ponds and lakes, McCombie and Wile (1971) found P. pectinatus growing in waters of wide specific conductance range and spanning the complete range of Secchi transparencies from 0.9 to around 5.7 m. This species may be found in waters high in suspended sediment and organic pollution and is often rooted in silty sediments (Butcher, 1933; Hynes, 1970; Haslam, 1978; Ozimek, 1978). The essentially linear leaves have been observed to be relatively free of the silt blanket which tends to cover submersed macrophytes in waters high in suspended sediments as discussed previously (McCombie and Wile, 1971; Schiemer and Prosser, 1976).

The data points for Ceratophyllum demersum (Figure 8h) indicate a distribution at somewhat greater depths than other species for water bodies with Secchi depths less than 5 m. This suggests a degree of shade tolerance for this species which will be discussed in more detail in a later section. For Elodea canadensis, the linearity between maximum depth and Secchi transparency is remarkable. The depth record of 12 m in Lake George, New York (Sheldon and Boylen, 1977) is the greatest depth reported for submersed angiosperms. Summer water temperature to 12 m ranged from 22-25°C in Lake

George. Light transmission to 12 m during the summer was about 10 percent of incident and the water column and sediments were aerobic at least to 12 m water depth. Thus, these factors probably were not limiting the maximum depth of growth. Rather, hydrostatic pressure is important in limiting the depth of growth of deep water species in Lake George. Elodea canadensis was somewhat more resistant to excess pressure than two other species studied by Ferling (1957). A number of depth records in Figure 7 were for Lake George.

The linear pattern between maximum depth and Secchi transparency for Elodea canadensis differs from a tendency for some of the other species, such as Myriophyllum spicatum (Figure 8e), Vallisneria americana (Figure 8f), Najas guadalupensis (Figure 8g), and the Potamogeton subsection Perfoliati group (Figure 8i), to reach a plateau at 6 to 7 m depth. This plateau indicates that hydrostatic pressure rather than light availability controls maximum depth distribution.

Turbidity Tolerance Index

When the maximum depths for submersed angiosperms of Figure 7 are plotted against their Secchi depths, a linear relationship is apparent at shallow depths for most species (Figure 8). This suggests that, in the range of around 2.5 m Secchi depth or less, turbidity is an important factor affecting maximum depths of growth. It follows that if a species is found in the deeper areas in water bodies with 2.5 m Secchi depths or less, the species would have a degree of turbidity tolerance. More specifically, the higher the depth maxima to Secchi depth ratio in the turbidity-stressed systems, the higher the turbidity tolerance of the species. This ratio, along with related information, is given in Table 1 for species of Figure 8. Species with higher turbidity tolerance indices are better adapted for survival under conditions of low light transmission.

The absence of Potamogeton praelongus in the systems with turbidity stress typifies potamogetons that are mainly restricted to northern areas as discussed previously. The low ratio for Eleocharis acicularis is not surprising; the depth distribution of this species does not correlate with Secchi transparency. Elodea canadensis is apparently sensitive to turbidity, even though it may grow at great depths where turbidity is low. Perhaps the effects of suspended particles on light quality reaching the plants is especially important for this species. Of the remaining species Ceratophyllum demersum, Vallisneria americana, Najas guadalupensis, and P. pectinatus have the highest turbidity tolerances. The mean depth of Ceratophyllum demersum is greater than that of other species (Figure 8).

Thus, it appears that not all species tolerant to low levels of light and growing at great depths in clear lakes will be successful in colonizing aquatic ecosystems of high turbidity. These exceptions may be species that are sensitive to factors such as eutrophication, substrate type, siltation of leaves, or light quality, rather than just the quantity of light. Nevertheless, the turbidity tolerance index provides an approximation of the relative resilience of several species to turbidity stress and their rank is

Table 1. Turbidity Tolerance Index for Selected Species of Figure 7
Expressed as the Ratio of Depth Maxima to Secchi Depth
Where Secchi Depth is 2.5 m or Less

Species	No. Systems: Secchi \leq 2.5 m	Total No. Systems	Turbidity Tolerance Index
<u>Potamogeton praelongus</u>	0	11	0
<u>Eleocharis acicularis</u>	2	7	0.5
<u>Elodea canadensis</u>	7	14	1.1
<u>Potamogeton s.s. Perfoliati</u>	9	17	1.5
<u>Najas flexilis</u>	3	11	1.7
<u>Myriophyllum spicatum</u> ^a	11	40	1.7
<u>Potamogeton pectinatus</u>	9	22	2.0
<u>Najas guadalupensis</u>	5	6	2.2
<u>Vallisneria americana</u>	6	17	2.4
<u>Ceratophyllum demersum</u>	2	11	2.8

^aFrom data for lakes of southern Ontario, Canada. Twenty-three sampling stations were in Georgian Bay of Lake Huron with the rest from various other lakes (I. Wile, in preparation).

supported by observations on distribution in nature. Additional data are needed to firmly establish the relationship between submersed species and turbidity.

PHOTOSYNTHESIS AND GROWTH IN RESPONSE TO LIGHT

It is apparent from the foregoing discussion that some macrophyte species have an affinity for deeper or more turbid waters while others tend to be restricted to conditions of higher light intensities. It would be impossible from the data given above to classify all species as being either shade tolerant or high light requiring although the approach used in Table 1 is promising. Rather we will examine the experimental evidence available for a few species to see if it provides further insight to the possible light control of macrophyte zonation and turbidity tolerance.

Many of the experiments reported in the literature on apparent photosynthetic rates of submersed macrophytes relate to the light intensity at which the photosynthetic system is saturated. The lowest irradiance necessary to achieve the maximum rate of photosynthesis (saturation) provides a valuable point of reference for comparing species. Since the subject of this review is concerned more with the response of macrophytes to reduced levels of light, these experiments might appear irrelevant. However, where light is only occasionally limiting due to shading by high turbidity waters, the competitive advantage of species with a high photosynthetic efficiency may help to explain their occurrence. Such conditions might occur in shallow zones of lakes or normally clear rivers with pulses in turbidity due to storms, dredging, high runoff, etc. Moreover, it might be proposed that species with high light saturation correspondingly have lower photosynthetic rates at low light levels and higher compensation points than shade adapted species.

The compensation point of light, i.e., where photosynthesis and respiration are in balance, should limit the lower depth distribution of a species. In laboratory and field experiments where compensation points are measured, they can only approximate depth distributions in nature. This is partly because experiments are normally of short duration, while under natural conditions plants respond to a seasonal range of light conditions (turbidity, day length, solar angle, etc.). Furthermore, experiments are normally with active apical portions of plants and do not reflect respiratory utilization of photosynthate by older stem portions and underground parts. There is another problem with extrapolating low irradiance experiments in the laboratory to deep water conditions. In deep clear lakes, selective light absorption by water (red region) and by organic compounds (blue region) may be as great a factor in photosynthesis as reduction in total irradiance (Figure 6). Research appears to be lacking on this problem for aquatic macrophytes.

A further problem with interpretation of the experiments discussed below is the lack of consistency among experiments. For example, some workers report light values as illuminance (lux or foot candles) while others more appropriately use irradiance ($\text{cal/cm}^2 \cdot \text{hr}$ or $\mu\text{einstein/m}^2 \cdot \text{sec}$). The two expressions are not interconvertible because illuminance does not take into account the variation in energy distribution of different spectral regions. Moreover, there are problems with differences in temperature, light source, enclosed biomass, and inorganic carbon availability both within and among experiments. Finally problems are associated with accumulation and utilization of oxygen in intercellular spaces (lacunae) of submersed plants (Hartman and Brown, 1967). However, to the extent possible, these experiments will be discussed as they may relate to macrophyte depth zonation and turbidity tolerance.

Laboratory Experiments

In a series of laboratory experiments, Gessner (1938) determined light saturation for photosynthesis in six submersed species. Four of the species, Ceratophyllum demersum, Cabomba aquatica, Hottonia palustris, and Ranunculus aquatilis, appeared to saturate at approximately 10,000 to 40,000 lux. This low light saturation of C. demersum is in agreement with its high turbidity tolerance index (depth maximum to Secchi depth ratio) reported in Table 1.

The other two species, Elodea crista and Potamogeton perfoliatus, did not saturate within the range of light intensities used. It would appear that particularly for P. perfoliatus light saturation was somewhat above 80,000 lux. This concurs somewhat with the low turbidity tolerance index of Potamogeton subsection Perfoliati of Table 1. The photosynthetic curves for C. demersum and C. aquatica appear to increase quite rapidly at the lower light intensities relative to the other species.

Boyd (1975) reported changes in net photosynthesis of 1 g samples with increasing light intensity. Photosynthesis in three of the species reached light saturation at about 10,000 lux (Eleocharis acicularis, Elodea densa, Najas flexilis), while light saturation occurred at 15,000 lux for Potamogeton sp. and 20,000 lux for Ceratophyllum demersum. None of the species required more than 9,000 lux for 50 percent of maximum photosynthesis. These results are in general agreement with those of Gessner (1938) except for the two species that he reported which did not reach maximal photosynthesis.

Comparative photosynthetic rates for four species of submersed plants reported by Van et al. (1976) did not differ greatly in irradiance required for saturation (600-700 $\mu\text{E}/\text{m}^2\cdot\text{sec}$), but light compensation points differed substantially. The compensation point for Hydrilla verticillata was lowest, at 15 $\mu\text{E}/\text{m}^2\cdot\text{sec}$, Cambomba caroliniana was highest at 55 $\mu\text{E}/\text{m}^2\cdot\text{sec}$, while Myriophyllum spicatum and Ceratophyllum demersum were intermediate at 35 $\mu\text{E}/\text{m}^2\cdot\text{sec}$. Even though H. verticillata and C. demersum had high to medium tolerances, respectively, to low light levels, their maximal photosynthetic rates were higher than the other two species per unit of chlorophyll content. It would appear then that some species are adapted to a wide range of light conditions, being able to tolerate quite low levels of light and have high photosynthetic capacities at high light levels. Since H. verticillata exhibits this capability, this would explain its rapid biomass production under favorable light conditions as well as its large standing crops where self shading is high (Nall and Schardt, 1978). Carr (1969a, b) also characterized C. demersum as a shade plant, being adapted to low levels and saturating at about 40,000 lux in flasks and about 15,000 lux under artificial stream conditions. She observed maximum photosynthesis in plants collected from 5 m depth in Lake Ohakuri, New Zealand, where light intensity was about 2 percent of surface. However, Meyer and Heritage (1941) found this species to have maximum photosynthesis at the surface of Lake Erie. As Carr (1969b) pointed out, this may have been a result of using only plants collected from the surface rather than incubating them at light intensities at the depth from which they were collected. Further evidence for shade adaptation of Ceratophyllum demersum relative to other species was reported by Guilizzon (1977) for Lake Wingra, Wisconsin. Saturation of photosynthesis occurred at 250 $\mu\text{E}/\text{m}^2\cdot\text{sec}$ compared with 800 $\mu\text{E}/\text{m}^2\cdot\text{sec}$ for Myriophyllum spicatum.

It is uncertain to what extent these short term (usually ≤ 1 hour) laboratory experiments, in which dissolved oxygen production rates are measured, are comparable to longer term studies in which growth is measured by increases in length or biomass. For example, Blackburn et al. (1961) reported that Elodea densa (Planch) Caspary has a low light requirement and that long-term

growth (12 weeks under fluorescent lamps) was optimum at about 100 foot candles. Above 125 foot candles rapid chlorosis and death occurred. In comparison, Heteranthera dubia had a high light requirement with optimum intensity at 590 foot candles. Long-term studies would appear to take into account differing abilities of species to adapt to light intensities.

A fundamental difference in response to light saturation by sun leaves (acclimated under high light intensity) and shade leaves was reported by Gessner (1938) for several species of submersed macrophytes. Proserpinaca palustris, Elodea crista, and Potamogeton densus all showed light saturation at about 40,000 lux or less, while the sun leaves continued to show a near linear photosynthetic response to increasing light above that level. Similarly, the emergent leaf form of the heterophyllous Proserpinaca palustris saturated at higher light levels than the submersed leaf form. This suggests that not only are there inherent differences in light saturation levels among species, but that there is considerable plasticity within a species depending on exposure to light conditions prior to experimentation.

This problem was addressed by Spence and Chrystal (1970a,b) who showed that some Potamogeton species had a greater reduction in photosynthesis with reduced irradiance than others. There was a tendency for these species to be restricted to the more shallow zones of lakes, and thus be less shade tolerant, than the ones that underwent less reduction in photosynthesis. The mechanism for the adaptation of shade species appeared to be related to lower leaf respiration and reduced thickness under low light conditions. These features allow net photosynthesis to continue under low irradiance. In contrast, the thicker leaves of sun species were more efficient at higher irradiances.

Otto and Enger (1960) maintained submersed plants (Potamogeton pectinatus, P. nodosus, Elodea canadensis) in tanks with varying concentrations of suspended sediment. Growth reductions relative to controls were 20 to 40 percent for sediment concentrations of 50 ppm. The amount of growth reduction was approximately linear with increasing sediment concentrations up to about 1,250 ppm. Abnormalities in growth at higher concentrations over the 4-week growth period included elongation of stem internodes and chlorosis of stems and basal submersed leaves. Potamogeton pectinatus appeared to be less tolerant to suspended sediments than the other two species and the authors attribute this to its lower leaf area. This does not agree with field observations (Table 1, Figure 7) which show it to be reasonably turbidity tolerant.

This research is of interest because it is the only known study in which suspended sediment concentrations have been manipulated to observe growth responses of submersed vascular plants. However, the authors conclude that "Sediment concentrations greater than 1,250 ppm would be necessary to cause plant growth reductions that might be considered critical to the plants' ability to survive." This statement should not be taken out of the context of the experiments conducted and applied to field conditions. First, the plants were growing in only about 60 cm of water and the results may apply only to shallow water conditions. Secondly, and probably more importantly, many natural stands of submersed vascular plants may be living near their

limit of tolerance owing to physical, chemical, and biological factors discussed previously. Additional light reduction due to turbidity, even at the lowest levels of suspended sediment used in these experiments (50 ppm), may exceed the threshold of tolerance for plant communities already subjected to other stress factors.

Field Studies

Few field studies have been conducted to determine photosynthetic and growth responses to light. Because of the problems discussed above as well as changing light conditions within the course of a day or season, such experiments are difficult to interpret and extrapolate to field observations of plant distribution. However, they may have some value in a relative sense when several species are compared. For example, Meyer et al. (1943) determined the compensation depth for shoot tips of several submersed species in Lake Erie. Compensation light intensity was approximately 1 percent of the intensity measured at 5 cm depth for Elodea canadensis, Potamogeton richardsonii, Vallisneria americana and Heteranthera dubia. The value for Najas flexilis was somewhat higher at 2.6 percent.

Photosynthesis and respiration in submersed species were studied in detail by Ikusima (1965, 1966, 1967). He showed that photosynthesis decreased progressively from the upper part to the basal parts of community of Potamogeton crispus and Vallisneria asiatica Miki, but that respiration was fairly constant throughout (Ikusima, 1965). Photosynthesis in Vallisneria denserulata Makino beds varied considerably from day to day depending on whether the weather was clear, cloudy, or rainy (Ikusima, 1966). As expected, the compensation depth may vary from hour to hour during the day even though the light compensation point of the plants may remain constant. Monthly differences occurred as well (Ikusima, 1967). Interception of light by apical portions of shoots, which reduces considerably the rate of photosynthesis of lower portions, results in a large respiratory demand where biomass is generally largest. Communities during overcast or rainy days may even have a negative net organic matter budget.

The results of the laboratory experiments and field studies cited above demonstrate a number of problems in interpreting instantaneous measurements of photosynthesis. Species can be ranked according to their capacity for photosynthesis at light saturation intensities, which may be indicative of their success in competition if light saturation intensities persist under field conditions. However, distribution and abundance of aquatic macrophytes in nature reflects the totality of the forcing functions that affect macrophyte growth, of which light is just one.

RESPONSES OF SUBMERSED PLANTS TO ECOSYSTEM CHANGE

COMMUNITY RESPONSES TO THE DURATION OF PERTURBATION

Factors affecting the growth and distribution of submersed plants have been discussed. In this section one example of short term and one of long term fluctuations in macrophyte community structure as related to natural and anthropogenic stresses will be considered. Short term changes described in the literature are often related to a single perturbation with observations before and after the event. The observation period may vary from weeks as for the study by Bilby (1977) of changes in cover and areal distribution of plants following a stream spate to several years as for changes in macrophyte communities in the Currituck Sound of North Carolina (Davis, in preparation). On the other hand, some lakes in the northern U.S.A. have been studied sporadically for over a half century as for the Iowa Great Lakes (Crum and Bachmann, 1973).

Compared with responses of submersed plants to short term perturbations which are usually associated with increased suspended sediment loads in the water, long term changes in plant responses generally are harder to relate to specific environmental changes. Although changes in parameters with time, such as water transparencies, have been found during long term studies, short term changes associated with meteorological conditions and human activities such as dredging may be generally more important in effecting changes in submersed plant populations.

Short Term Perturbations

The observations of Steenis (1947) of the decimation of submersed macrophytes in Reelfoot Lake, Tennessee, following heavy rains in June 1945 represent changes which may occur following a single perturbation. The water level rose and extensive siltation resulted from erosion of hills around the lake. Steenis' observations are summarized in Table 2. Ceratophyllum demersum was the dominant submersed plant before the rains, but it appeared to succumb to increased turbidity and wind action that resulted from increased fetch as the water level rose. Lind and Cottam (1969) reported that C. demersum in University Bay of Lake Mendota, Wisconsin, "anchors poorly" in the sediment and was restricted to areas of low turbulence. Potamogeton pectinatus remained fairly abundant in places through 1945, but was limited in part by feeding activities of carp and competition with filamentous algae. In 1946 growth of P. pectinatus

Table 2. Changes in Submersed Macrophyte Populations in Reelfoot Lake, Tennessee (Steenis, 1947)

Species	Before 1945	Summer 1945	1946
<u>Ceratophyllum demersum</u>	Dominant, many pure stands	Fragmentary, but some extensive beds in sheltered areas	Showing definite signs of again dominating
<u>Najas guadalupensis</u>	Limited and suppressed growth in <u>C. demersum</u>	Scattered, sparse in much of lake	Extensive cover in some areas
<u>Potamogeton pusillus</u>	Prominent in some areas but dominated by <u>C. demersum</u> later in season	Scattered, sparse in much of lake	Extensive cover in some areas; more aggressive than <u>N. guadalupensis</u>
<u>Zannichellia palustris</u>	Suppressed fragmentary growth in limited areas	Scattered, sparse in much of lake	Extensive growth; expansive and pioneer
<u>Potamogeton nodosus</u>	Scattered small beds	Scattered, sparse in much of lake; set back and slightly redistributed	Spots of existing growth increased about 10-fold
<u>Potamogeton pectinatus</u>	Scattered small beds; greater range than <u>P. americanus</u>	Scattered, sparse in much of lake; fairly abundant in one area but set back by carp action and overcovering with algae	Luxuriant beds in much of the lake; largest stands ever observed by Steenis for lake
<u>Heteranthera dubia</u>	Limited; two areas		Plants that had survived were slowly recovering
<u>Cabomba caroliniana</u>	Limited; one area	Set back	New growth in an additional area
<u>Utricularia vulgaris</u>	Mainly in shallow <u>Nuphar advena</u> dominated areas		Continued without change

was more luxuriant and widespread than Steenis had ever observed before. Accelerated growth of Najas guadalupensis and P. pusillus also occurred in some regions of the lake in 1946. Potamogeton pusillus was described as the more aggressive of the two. Ceratophyllum demersum came back strongly in the year following the rains while there was a dramatic growth and spread of Zannichellia palustris. Here then, virtual elimination of the dominant species led to changing niches with rapid recovery and increase in macrophyte diversity.

Other short term changes in species composition and/or biomass have been reported for a shallow pond (Stuckey, 1971), a shallow flood plain (Jackson and Starrett, 1959), a lake (Oglesby et al., 1976), and a reservoir (Peltier and Welch, 1970). In all of these cases an increase in suspended sediment turbidity resulted from changing environmental conditions.

Long Term Perturbations

Perhaps the most significant study of long term changes in submersed macrophyte populations was that by Crum and Bachmann (1973) of lakes of the Iowa Great Lakes region. They took advantage of an excellent opportunity to compare the submersed macrophytes in six essentially contiguous lakes which now have varying trophic states. The time element was added to their analysis through reference to three other studies, the first of which was in 1894. Depth distributions of submersed macrophytes given by Crum and Bachmann are included in Figure 7. These data were especially valuable in establishing relationships at the low end of the Secchi depth scale for several individual species (Figure 8).

At the time of the study in 1972, some of the northern potamogetons remained in Lake West Okoboji (4.2 m Secchi depth) and Big Spirit Lake (2.8 m Secchi depth) while none were in the more turbid lakes (0.7 to 1.6 m Secchi depth range) (Table 3). Generally, the species remaining in the more turbid lakes were those which have been established as turbidity tolerant (Table 1); however, these same species also were found in the clearer lakes. These observations suggest that the northern potamogetons are sensitive to turbidity and associated changes while plants that are turbidity tolerant may thrive under a variety of conditions.

The initial invasion of the clearest lake by Potamogeton crispus is surprising since it often grows in disturbed or eutrophic systems. Migration to the other lakes might be expected in the future. The presence of Ruppia maritima in only one lake is also of interest. Since this species is normally found in saline environments (cf. Metcalf, 1931), a comparison of salinities of these lakes would be of interest. Indeed, further analyses of physical and biological parameters that might affect the distribution of submersed macrophytes seems warranted.

Based on a study in which macrophytes of Lake East Okoboji were compared with a 1915 survey, Volker and Smith (1965) suggested a number of factors responsible for the observed changes. These include nutrient enrichment from agricultural runoff and from sewage leading to algal blooms, siltation from

Table 3. Long Term Changes in Macrophyte Populations in Lakes and Bays in Northern United States.

	Iowa Great Lakes (1894-1972)			
	Lake West Okoboji	Big Spirit Lake	Lake East Okoboji	Gar (three lakes)
Long term presence:	<p><u>Ceratophyllum demersum</u>^{ab}</p> <p><u>Elodea canadensis</u></p> <p><u>Heteranthera dubia</u></p> <p><u>Myriophyllum exalbescentis</u>^{ab}</p> <p><u>Najas flexilis</u>^b</p> <p><u>Potamogeton amplifolius</u></p> <p><u>P. natans</u></p> <p><u>P. nodosus</u></p> <p><u>P. pectinatus</u></p> <p><u>P. praelongus</u></p> <p><u>Potamogeton sub. sec.</u></p> <p><u>Pusilli</u></p> <p><u>P. richardsonii</u>^b</p> <p><u>P. zosteriformis</u></p> <p><u>Ranunculus longirostris</u></p> <p><u>Vallisneria americana</u>^b</p> <p><u>Zannichellia palustris</u></p>	<p><u>Ceratophyllum demersum</u>^b</p> <p><u>Myriophyllum exalbescentis</u>^a</p> <p><u>Najas flexilis</u>^b</p> <p><u>Potamogeton amplifolius</u></p> <p><u>P. illinoensis</u></p> <p><u>P. nodosus</u></p> <p><u>P. pectinatus</u></p> <p><u>P. praelongus</u></p> <p><u>Potamogeton sub. sec.</u></p> <p><u>Pusilli</u></p> <p><u>P. richardsonii</u>^{ab}</p> <p><u>P. zosteriformis</u></p> <p><u>Ruppia maritima</u>^b</p> <p><u>Vallisneria americana</u>^{ab}</p> <p><u>Zannichellia palustris</u></p>	<p><u>Ceratophyllum demersum</u>^a</p> <p><u>Elodea canadensis</u></p> <p><u>Heteranthera dubia</u></p> <p><u>Najas flexilis</u></p> <p><u>Potamogeton pectinatus</u></p> <p><u>Potamogeton sub. sec.</u></p> <p><u>Pusilli</u></p> <p><u>P. richardsonii</u></p> <p><u>Vallisneria americana</u></p> <p><u>Zannichellia palustris</u></p>	<p><u>Ceratophyllum demersum</u></p> <p><u>Elodea canadensis</u></p> <p><u>Potamogeton pectinatus</u></p> <p><u>P. richardsonii</u></p> <p><u>Vallisneria canadensis</u></p>
Disappeared:	<p><u>Megalodonta (Bidens) beckii</u></p> <p><u>Potamogeton diversifolius</u></p> <p><u>P. epiphydrus</u></p> <p><u>P. gramineus</u></p>	<p><u>Elodea canadensis</u></p> <p><u>Megalodonta (Bidens) beckii</u></p> <p><u>Potamogeton diversifolius</u></p> <p><u>P. epiphydrus</u></p> <p><u>P. natans</u></p>	<p><u>Potamogeton amplifolius</u></p> <p><u>P. diversifolius</u></p> <p><u>P. epiphydrus</u></p> <p><u>P. gramineus</u></p> <p><u>P. natans</u></p> <p><u>P. nodosus</u></p> <p><u>P. praelongus</u></p> <p><u>P. zosteriformis</u></p> <p><u>Megalodonta (Bidens) beckii</u></p> <p><u>Myriophyllum exalbescentis</u></p> <p><u>Ranunculus longirostris</u></p>	<p><u>Heteranthera dubia</u></p> <p><u>Hippuris vulgaris</u></p> <p><u>Megalodonta (Bidens) beckii</u></p> <p><u>Myriophyllum exalbescentis</u></p> <p><u>Najas flexilis</u></p> <p><u>Potamogeton amplifolius</u></p> <p><u>P. natans</u></p> <p><u>P. nodosus</u></p> <p><u>P. praelongus</u></p>
Recent Adventive:	<p><u>Potamogeton crispus</u></p> <p><u>P. illinoensis</u></p>	<p><u>Heteranthera dubia</u>^b</p>	<p><u>Potamogeton sub. sec.</u></p> <p><u>Pusilli</u></p> <p><u>Zannichellia palustris</u></p>	

Table 3 (Concluded)

Condition	Put-in-Bay Harbor, Ohio (1898-1967)	University Bay, Wisconsin (1912-1965)	Green Lake, Wisconsin (1921-1971, 74)	Lake Wingra, Wisconsin (1929-1968, 69)
Long term presence:	<u>Butomus umbellatus</u> <u>f. vallisnerifolius</u> <u>Ceratophyllum demersum</u> <u>Heteranthera dubia</u> ^a <u>Myriophyllum exalbescens</u> <u>Potamogeton bertholdii</u> <u>P. crispus</u> <u>P. pectinatus</u> ^a <u>P. richardsonii</u> ^a <u>Vallisneria americana</u> ^b <u>Zannichellia palustris</u>	<u>Ceratophyllum demersum</u> ^b <u>Elodea canadensis</u> <u>Heteranthera dubia</u> <u>Najas flexilis</u> <u>Myriophyllum exalbescens</u> ^b <u>Potamogeton crispus</u> <u>P. pectinatus</u> <u>P. richardsonii</u> <u>P. zosteriformis</u> <u>Vallisneria americana</u> ^{a,b} <u>Zannichellia palustris</u>	<u>Ceratophyllum demersum</u> ^a <u>Chara sp.</u> <u>Elodea canadensis</u> <u>Heteranthera dubia</u> <u>Myriophyllum spicatum</u> <u>Najas flexilis</u> <u>Potamogeton amplifolius</u> <u>P. gramineus</u> <u>P. natans</u> <u>P. pectinatus</u> <u>P. richardsonii</u> <u>P. zosteriformis</u> <u>Ranunculus sp.</u> <u>Vallisneria americana</u> ^b <u>Zannichellia palustris</u>	<u>Ceratophyllum demersum</u> <u>Elodea canadensis</u> <u>Heteranthera dubia</u> <u>Myriophyllum spicatum</u> <u>Najas flexilis</u> <u>Potamogeton crispus</u> <u>P. foliosus</u> <u>P. natans</u> <u>P. pectinatus</u> <u>P. richardsonii</u> <u>P. zosteriformis</u> <u>Ranunculus longirostris</u> <u>Utricularia vulgaris</u>
Disappeared:	<u>Elodea canadensis</u> <u>Megalodonta (Bidens) beckii</u> <u>Najas guadalupensis</u> <u>N. flexilis</u> ^a <u>Potamogeton amplifolius</u> <u>P. filiformis</u> <u>P. foliosus</u> <u>P. friesii</u> <u>P. gramineus</u> <u>P. natans</u> <u>P. nodosus</u> <u>P. perfoliatus var.</u> <u>bupleuroides</u> <u>P. praelongus</u> <u>P. pusillus</u> <u>P. zosteriformis</u> ^a	<u>Potamogeton amplifolius</u> ^a <u>P. illinoensis</u> <u>P. natans</u> <u>P. nodosus</u> <u>P. praelongus</u>	<u>Myriophyllum verticillatum</u> <u>var. pectinatum (perhaps)</u> ^a <u>Potamogeton foliosus</u>	<u>Potamogeton amplifolius</u> <u>P. friesii</u> <u>P. illinoensis</u> <u>P. praelongus</u> <u>Vallisneria americana</u> ^a
Recent Adventive	<u>Elodea nuttallii</u>	<u>Potamogeton foliosus</u>	<u>Myriophyllum spicatum</u> ^b <u>Potamogeton friesii</u>	<u>Myriophyllum spicatum</u> <u>(perhaps)</u> <u>Potamogeton crispus</u> <u>(perhaps)</u>

^a Dominant or subdominant in an earlier survey.^b Dominant or subdominant at last survey.

agriculture, the use of algicides, depletion of dissolved oxygen, and fluctuations in water level. Crum and Bachmann (1973) suggested that stabilization of water levels in some of the lakes may have led to the demise of certain submersed macrophytes. The possible effects of herbicides in areas of intense agriculture might also be considered (Correll et al., 1978).

Long term changes in submersed plants for other systems are summarized in Table 3. Environmental degradation associated with shoreline development and intense use of waterways in and around Put-in-Bay Harbor on an island in Lake Erie, Ohio, led to a drastic decrease in macrophyte presence and density over 70 years (Stuckey, 1971). Changes in the submersed macrophyte community over the period described by Stuckey did not begin with a pristine environment which gradually deteriorated due to human activities. Poor agricultural practices on the island apparently contributed to a heavy suspended sediment load in the study area from the beginning of the studies (Thorndale, 1898 as cited in Stuckey, 1971). Stuckey cites Pieters (1901) as reporting that in 1898 it was impossible to see plants in one area deeper than around 0.6-0.9 m due to turbidity. Stuckey suggested that the demise of the plants over time was related to a combination of warming of the water, increased turbidity and decreased dissolved oxygen. Increased turbulence due to extensive bulkheading along the shore could also have been a factor. In the Pamlico River, North Carolina, submersed macrophytes were usually limited to a narrow band in the deeper part of the littoral where bulkheading was extensive (Davis and Brinson, 1976).

Lind and Cottam (1969) studied the submersed macrophytes of University Bay of Lake Mendota, Wisconsin in 1966 and compared their results with those of surveys made by Denniston (1921), Rickett (1922), and others. Compared with Rickett's data, they found that the biomass of Myriophyllum exalbescentis (or perhaps M. spicatum) had increased drastically while that of Vallisneria spiralis decreased and Ceratophyllum demersum increased (Table 3). Lind and Cottam (1969) suggested that eutrophication caused the changes observed in University Bay.

Bumby (1977) compared the submersed macrophyte biomass and distribution in Green Lake, Wisconsin, in 1971-1974 with that in 1921 (Rickett, 1924). As for University Bay (Lind and Cottam, 1969), Myriophyllum (M. spicatum) had become dominant, but relative biomass (46 percent) was not as great as for M. exalbescentis in University Bay. Secchi depths were not given, but Bumby suggested that there had been no change measured in light transmission since 1942. However, decreased light due to suspended sediments and seston in the littoral and the abundance of the filamentous alga, Cladophora sp., were suggested as possible factors affecting the observed changes.

Lake Wingra is yet another Wisconsin lake in which Myriophyllum has become dominant (Nichols and Mori, 1971). The relative frequency of M. spicatum was 68 percent and no other submersed species had a relative frequency of over 10 percent. The authors suggested that the lake was once dominated by potamogetons and Vallisneria spiralis. The species found in 1968-1969 were much the same as described for the other Wisconsin lakes (Table 3).

Vallisneria americana and northern potamogetons had disappeared by 1929, as determined by a herbarium survey. Carp were introduced in the late 1800's and practically eliminated submersed macrophytes from the lake from the 1920's through 1955 (Baumann et al., 1974). The demise of V. americana was associated with the carp infestation, apparently due to increased turbidity.

All the long-termed changes described thus far are for northern lakes which apparently had no rosulate populations typical of sandy, shallow areas of some northern oligotrophic lakes. Flora of such lakes has been reported for northern Wisconsin (i.e. Steenis, 1932; Wilson, 1935; Potzger and Van Engel, 1942), New Hampshire (Moeller, 1975), Scottish Lochs (Spence, 1967) and English Lakes (i.e., Pearsall, 1920) as well as other northern European countries (Hutchinson, 1975).

Hutchinson (1975) suggested that the oligotrophic Weber Lake in northern Wisconsin had the simplest known macrophyte community for northern lakes of moderate altitudes and latitudes. Potzger and Van Engel (1942) found that all species growing in Weber Lake were basically rooted in sandy sediments and suggested that growth of smaller plants (eight of nine species found) in deeper waters was restricted by a cover of organic sediments. Even in the observed depth ranges, Myriophyllum tenellum and Isoetes macrospora Dur. were frequently etiolated up to near the tips due to sediment cover. Other low growing species included Elatine minima, Eriocaulon septangulare, Juncus pelocarpus f. submersus, Gratiola lutea f. pusilla and Lobelia dortmanna.

In comparing three northern Wisconsin lakes of varying trophic states, Wilson (1935) found that most of the rosulate forms were not present in the eutrophic lake. In the other lakes they were present in only trace amounts. Some of the northern potamogetons were present at very low relative biomasses where Najas flexilis was dominant with Potamogeton richardsonii a weak sub-dominant.

From 1821 through 1894, several rosulate forms disappeared from Loch Leven, now eutrophic (Jupp et al., 1974). Several of the species described here as northern potamogetons were present, but had disappeared by 1910. By 1966 Ceratophyllum demersum and perhaps Myriophyllum spicatum had disappeared. Potamogeton pectinatus and Zannichellia palustris were adventive by 1959 and P. crispus was first reported in 1966.

To summarize the long-term changes in submersed macrophyte communities described above, a survival index has been developed for plants of the northern lakes of Table 3 (Lake West Okoboji and Big Spirit Lake were omitted since there was comparatively little change in submersed species). This is simply a ratio of the number of lakes in which a species was reported in earlier surveys to the number of lakes in which the species was present when last studied. The survival index was calculated for species which were originally found in three or more of the lakes. As for the turbidity tolerance index, other factors in addition to an increase in turbidity surely played a part in changes in plant populations observed. Survival indices calculated and turbidity tolerance indices from Table 2 are:

	<u>Survival Index</u>	<u>Turbidity Tolerance Index</u>
<u>Ceratophyllum demersum</u>	1.0	2.8
<u>Potamogeton pectinatus</u>	1.0	2.0
<u>P. richardsonii</u> (s. s. <u>Perfoliati</u>)	1.0	1.5
<u>Zannichellia palustris</u>	1.0	
<u>Elodea canadensis</u>	0.8	1.1
<u>Heteranthera dubia</u>	0.8	
<u>Vallisneria americana</u>	0.8	2.4
<u>Najas flexilis</u>	0.7	1.7
<u>Potamogeton zosteriformis</u>	0.6	
<u>P. foliosus</u>	0.3	
<u>P. gramineus</u>	0.3	
<u>P. natans</u>	0.3	
<u>P. amplifolius</u>	0.2	
<u>P. nodosus</u>	0.0	
<u>P. praelongus</u>	0.0	0.0

The tabulation of the survival indices merely emphasizes what is apparent in Table 3. The more cosmopolitan species tend to remain with ecosystem change while the northern potamogetons tend to disappear. As would be expected, there is a tendency toward a positive correlation between the survival index and the turbidity tolerance index.

CATEGORIES OF SPECIES BASED ON RESISTANCE TO ECOSYSTEM ALTERATION

An arbitrary grouping of submersed macrophytes based on their tendency to decrease in biomass or disappear with increasing alteration of ecosystems has been developed. Ecosystem alteration can be caused by a number of factors, but the net result is usually an increase in water turbidity. Five categories ranked roughly in order of increasing resistance to change are suggested as follows:

1. Rosulate species found mainly in northern lakes.

2. Northern potamogetons.
3. Tolerant species normally with low biomass in disturbed systems. These species may have relatively high biomass in pristine systems.
4. Tolerant species normally dominant or subdominant in disturbed systems.
5. Adventive species that appear in disturbed systems and may be dominant to rare.

Rosulate Species

Significant mixed rosulate populations appear to be restricted to oligotrophic northern lakes. Their absence elsewhere may be associated with factors related to increasing conductivity of the waters (Moyle, 1945) or, as Potzger and Van Engel (1942) suggested, increasing accumulations of finer sediments. Wilson (1935) said that several rosulate species should be considered terrestrial plants which "go aquatic" with submergence due to rising water level. These are normally small plants found in shallow waters and maximum depth distribution correlates poorly with Secchi depth (Figures 7 and 8). Myriophyllum tenellum, when present, is often included in rosulate populations since it is usually found with the rosulate species. Some of the rosulate species are:

Elatine minima

Isoetes macrocarpa

Eleocharis acicularis

Littorella americana

E. palustris

Lobelia dortmanna

Eriocaulon septangulare

Myriophyllum tenellum

Gratiola aurea f. pusilla

Northern Potamogetons

There is a preponderance of evidence that the potamogetons which are restricted to or are most widely distributed in northern areas do not survive the long-term changes that lead to eutrophication. Based primarily on the studies of the northern lakes, the potamogetons most sensitive to increasing eutrophication are:

Potamogeton amplifolius

P. natans

P. foliosus

P. nodosus

P. gramineus

P. praelongus

P. illinoiensis

P. zosteriformis

Of these species probably only P. foliosus can be considered truly cosmopolitan in distribution.

Potamogeton gramineus is one of the most sensitive of the northern potamogetons to ecosystem change. Stuckey (1971) cited Pieters (1901) as finding this species in 1898 in Put-in-Bay only on a bar where presumably the sediments were sandy and the water was shallow. In comparing three northern Wisconsin lakes, Wilson (1935) concluded that the comparatively low biomass of P. gramineus found in the most eutrophic lake was related to the greater accumulation of organic soils there. Wilson suggested that this species is a colonizer of primitive soils and disappears as the system develops. Bumby (1977) found P. gramineus outside her transects in Green Lake, Wisconsin in 1971, but was unable to find it again through 1973. Of the northern potamogetons, Potamogeton zosteriformis survives best. Just as the disappearance of P. gramineus is an indicator of early ecosystem changes, the continued presence of P. zosteriformis as other northern potamogetons disappear is an indication of further ecosystem change.

Tolerant Species Normally with Low Biomass in Disturbed Systems

Any species may be dominant in a part of a system or throughout the system depending on the conditions. However, for the systems reviewed here, there are some species which are resistant to ecosystem changes relating to decreased water transparency but which are commonly minor components of the systems. The species are:

Elodea canadensis

Potamogeton pusillus

Heteranthera dubia

P. richardsonii

Najas flexilis

Zannichellia palustris

Except for Najas flexilis which tends to have a northern distribution and Potamogeton richardsonii which belongs to a subsection (Perfoliati) which extends southward, the species in this group are widely distributed.

Tolerant Species Normally Dominant or Subdominant in Disturbed Systems

A few native species tend to maintain relatively high biomass in disturbed systems. These include:

Ceratophyllum demersum

Potamogeton perfoliatus
var. bupleuroides

Najas guadalupensis

Vallisneria americana

Ceratophyllum demersum and Potamogeton pectinatus are widespread, Vallisneria americana extends from south to north with rather spotty distribution, P.

perfoliatus var. bupleuroides forms the southern extension of the subsection Perfoliati and Najas guadalupensis is the southern counterpart of N. flexilis.

Potamogeton pectinatus is probably the most widespread and abundant of all North American submersed species. In the 1930's this species was the most important of the potamogetons as a food source of game ducks. Potamogetons as a group were the most important waterfowl food in six of the eight North American regions described by Martin and Uhler (1939). Only in two areas, the lower Mississippi and Gulf Coast regions, were other species of greater importance. The most used species there were Cyperus esculentus L. and Ruppia maritima, respectively. The resistance of P. pectinatus to suspended sediment loads and short and long-term ecosystem changes for the most part is consistent with the widespread abundance and importance of this species.

Adventive Species

As is now apparent, Myriophyllum spicatum has spread in the past quarter century to many areas in the United States and Canada where infestations often cause problems in human uses of lakes, streams, and reservoirs. As reviewed by Davis and Steenis (1973) intertwining mats of M. spicatum may adversely affect swimming, boating and various types of fishing. Quiescent waters in beds of M. spicatum may be conducive to breeding of mosquitos and decaying plants in windrows along the shore often cause obnoxious odors. There is confusion in distinguishing between M. spicatum and M. exalbesens but M. spicatum is likely the species involved in irruptions.

Observations in the Chesapeake Bay region (Steenis, 1970; Steenis et al., 1971) and Currituck Sound-Back Bay (Davis, in preparation) indicate that Myriophyllum spicatum is susceptible at least to short-term perturbations of the ecosystem. Reestablishment of the species as the dominant is highly variable and may not occur for many years.

Potamogeton crispus is another widespread adventive, especially in the northern region. This species is well established as an invader of eutrophic or disturbed waters, but in the Chesapeake Bay area it fluctuates widely with changing conditions (Steenis et al., 1971). Potamogeton crispus became a strong dominant in an Indiana lake and measures were taken to control it (McIntosh et al., 1978).

EFFECTS OF ENVIRONMENTAL ALTERATIONS ON SUBMERSED AQUATIC PLANTS

This section is intended to provide a better understanding of why reductions in submersed macrophytes occur and how specific environmental alterations may affect submersed plants. It should be emphasized at the outset that the capacity to predict changes in macrophyte communities due to natural or human induced environmental alterations is quite low. However, the examples of long term and short term changes in macrophyte communities just described show that some generalizations can be made that may allow some predictive capacity. Where natural episodes are responsible for changes, efforts toward conservation and management of submersed plant communities are not usually applicable. Thus management efforts must be directed toward human induced environmental changes. The condition of "overabundance" of aquatic macrophytes that may result from environmental manipulation or from invasion of adventive species will not be considered.

Since reduction in abundance of submersed plants can result from an array of factors, it would be instructive to examine how the forcing functions that cause these changes affect macrophyte communities. The diagram in Figure 9 is a conceptual model that separates these forces into three categories: light attenuation, toxicity, and biomass removal. Some of these may result in long term and others in short term changes of submersed plant communities. Light attenuation due to suspended sediments and eutrophication acts by reducing the energy available for photosynthesis. For suspended sediments, this may be either short term, as in the case of storms or floods, or long term, where the source of suspended sediments persists. Eutrophication is generally a long term effect since nutrient levels in aquatic ecosystems can persist long after the source of these nutrients are eliminated. Sediments of aquatic ecosystems often have a high capacity for storing elements critical to plankton growth and may continue to supply these nutrients to the water column after inputs to the system cease.

Toxicity due to herbicides, heavy metals, and other toxic substances acts by altering the metabolism of plants (Figure 9). The affinity of herbicides for small particles may result in the accumulation of these substances in the sediments as previously discussed, and effects may persist for long periods depending on the stability of the compounds in the environment and whether degradation products are also toxic.

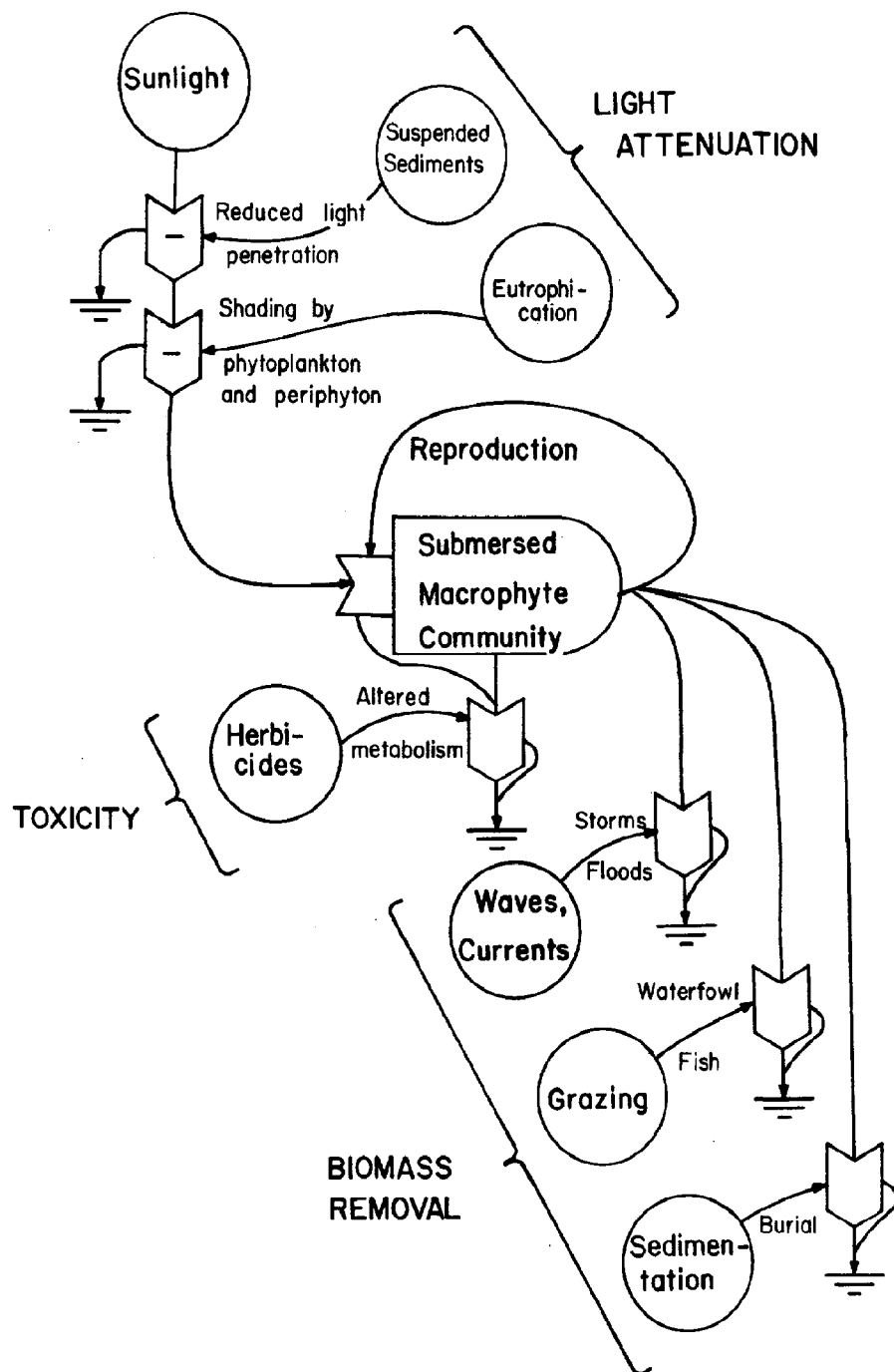


Figure 9. Conceptual model illustrating the effects of environmental forces on submersed aquatic macrophyte communities. These forces (circles) are separated into three categories of stress: light attenuation, toxicity, and biomass removal. Lines represent pathways of energy flow and bold arrows may either reduce flow (indicated by "-" sign) or accelerate flow. Thus all bold arrows represent stress on the macrophyte community, except for the one indicating a positive feedback of macrophyte reproduction. Symbols after Odum (1971).

Environmental factors resulting in biomass removal (Figure 9) are generally short term so long as the reproduction of aquatic plants is not impaired. Of these, only burial by sedimentation would normally be induced by human activities, such as dredging and instream mining, while the others are not amenable to control. Damage to macrophyte communities by the simultaneous occurrence of more than one stress should also be considered as a possibility.

With this model as a basis for understanding stresses on submersed plants, the separation of factors due to human and natural forces is facilitated. The management of submersed plants in relation to anthropogenic influences is confounded by a spectrum of problems associated with many variables such as the soil types which are disturbed (including aquasoils), the nature of the aquatic system (lotic vs. lentic, etc.) and the nature, time, and duration of the activity generating the pollution. The resiliency of the submersed macrophyte system under stress will be related to the ecological tolerance of the species present. For example, northern potamogetons are very sensitive to stresses associated with increased suspended sediments. As discussed in other sections, long term stresses may result in a greatly altered communities where exotic species often dominate. Under extreme stress by one factor or a multiplicity of several stresses, macrophyte communities may cease to exist.

Examples of human activities which may adversely affect natural systems and their possible effects on submersed plant populations are given in Table 4 along with possible plant community responses. These perturbations are a function of the stress factors discussed for Figure 9. Literature reviews relating to the effects of suspended sediments and sedimentation on aquatic organisms include Cordone and Kelley (1961), Hynes (1970), Baxter (1977), Morton (1977), Sorensen et al. (1977), and Stern and Stickle (1978). Estimates of the magnitude of pollution of aquatic ecosystems given in Table 4 were compiled mainly from information in these reviews. However, little information on the impact of changes in aquatic systems affecting submersed plants was presented. This paucity of research relating to clearcut examples of the effects of human activities on submersed plant communities is evident in this review as in others dealing with submersed plants (i.e., Spence, 1967; Westlake, 1968; Westlake, 1973; Wetzel and Hough, 1973). Evidence that long term environmental degradation associated with agricultural and urban pollution contributed to loss of many submersed species was given in a previous section. Some other examples of community response to stress are cited in Table 4.

Table 4. Evaluation of the Effects of Various Types of Environmental Alteration on Submersed Plant Communities

Environmental Alteration	Possible Effects				Community Resiliency
	Suspended Sediments	Eutrophication	Toxicity	Sedimentation	
Instream mining	Varies depending on bed sediments	Varies depending on bed sediments	Low	Plants buried by coarse sediments in a downstream gradient	Limited reestablishment after burial may be possible for forms like <u>Podostemum ceratophyllum</u>
Silviculture					
Selective harvest	Low	Low	Low	Low	Low level continuous silviculture may be conducive to macrophyte establishment
Clear cutting	High on short term	Low on long term	Low if herbicides not used	Variable	Impact ameliorated with reestablishment of ground cover
Logging roads	High	Low	Low	High	Erosion of ditches and roadbed contributes sediments
Urban					
Construction	High	High if soils are nutrient rich (i.3., phosphate)	Low	High	A few species such as <u>Potamogeton pectinatus</u> may survive high levels of urban pollution. a,b,c
Waste waters (secondary treatment)	Low	High	Low to High	Low	Recovery of diverse community possible unless sediments are toxic
Storm waters	High	High (continued)	High	Medium	

Table 4. (Continued)

Environmental Alteration	Possible Effects				Community Resiliency
	Suspended Sediments	Eutrophication	Toxicity	Sedimentation	
Agriculture	High	High	High	High	Adverse effects would be minimized with best available management techniques; substantial recovery of aquatic system would be expected from their application
Road construction	High	High if eroding soils are nutrient rich	Variable	High	Medium term pulse of pollution with community recovery expected except in areas of extreme siltation. Aquatic habitat may change due to "dam" effects of roadbed.
Stream channelization	High	High	Variable	High	Decreased shading conducive to increased plant growth but spate stress increased; gradual recovery of natural system possible without channel maintenance.
Dredging of navigation channels	High (short term and localized)	High	Varies with sediment content	Varies depending on spoil disposal techniques	Subsequent growth of submersed plants not buried may be enhanced by nutrient enrichment.
Nearshore mining	Variable	Variable	Variable	Variable	Effects vary according to mining method and control procedures.

(continued)

Table 4. (Concluded)

Environmental Alteration	Suspended Sediments	Possible Effects			Community Resiliency
		Eutrophication	Toxicity	Sedimentation	
Dams and impoundments					
Upstream (lake)	High	Variable	Low	High at mouth of rivers	Establishment of submer- sed plants depends on width of littoral as well as extent and periodicity of drawdown.
Downstream	High	Varies; some nutrient deple- tion in lake likely	Low	Low	Depends on discharge procedure. Extensive f plant beds may develop.
Bulkhead, jetties, groins	Low	Low	Low	Variable	Higher wave energy from bulkheads may reduce re- establishment; ^g lee side of jetties and groins conducive for growth

^aButcher (1933)

^bHaslam (1978)

^cOzimek (1978)

^dO'Rear (1975)

^eOdum (1963)

^fHynes (1970)

^gDavis and Brinson (1976)

REFERENCES

- Adams, M.S., J. Titus, and M. McCracken. 1974. Depth distribution of photosynthetic activity in a Myriophyllum spicatum community in Lake Wingra. *Limnol. Oceanogr.* 19:377-389.
- Anderson, M.G. and J.P. Low. 1976. Use of sago pondweed by waterfowl on the Delta Marsh, Manitoba. *J. Wildl. Mgmt.* 40:233-242.
- Arber, A. 1920. *Water Plants. A Study of Aquatic Angiosperms.* Cambridge Univ. Press. 436 pp. (Reprinted 1963 by Hafner Publ., N.Y.)
- Baker, J.P. and J.J. Magnuson. 1976. Limnological responses of Crystal Lake (Vilas County, Wisconsin) to intensive recreational use, 1924-1973. *Trans. Wisc. Acad. Arts Sci. Lett.* 64:47-61.
- Baumann, P.C., J.C. Kitchell, J.J. Magnuson, and T.B. Hayes. 1974. Lake Wingra, 1837-1973: A case history of human impact. *Trans. Wisc. Acad. Arts Sci. Lett.* 62:57-94.
- Baxter, R.M. 1977. Environmental effects of dams and impoundments. *Ann. Rev. Ecol. Syst.* 8:255-283.
- Bilby, R. 1977. Effects of a spate on the macrophyte vegetation of a stream pool. *Hydrobiologia* 56:109-112.
- Blackburn, R.D., J.M. Lawrence, and D.E. Davis. 1961. Effects of light intensity and quality on the growth of Elodea densa and Heteranthera dubia. *Weed Sci.* 9:251-257.
- Blackburn, R.D., P.F. White, and L.W. Weldon. 1968. Ecology of submersed aquatic weeds in south Florida canals. *Weed Sci.* 16:261-265.
- Blackburn, R.D., L.W. Weldon, R.R. Yeo, and T.M. Taylor. 1969. Identification and distribution of similar appearing aquatic weeds in Florida. *Hyalcinth Contr. J.* 8:11-21.
- Bole, J.B. and J.R. Allan. 1978. Uptake of phosphorus from sediment by aquatic plants, Myriophyllum spicatum and Hydrilla verticillata. *Water Res.* 12:353-358.
- Boltt, R.E., B.J. Hill, and A.T. Forbes. 1969. The benthos of some southern African lakes. Part I: Distribution of aquatic macrophytes and fish in Lake Sibayi. *Trans. Roy. Soc. S. Afr.* 38:241-248.
- Bourn, W.S. 1932. Ecological and physiological studies on certain aquatic angiosperms. *Contrib. Boyce Thompson Inst.* 4:425-496.
- Boyd, C.E. 1975. Competition for light by aquatic plants. *Agr. Exp. Sta. Cir.* 215. Auburn Univ. 19 pp.

- Brinson, M.M. and G.J. Davis. 1976. Primary productivity and mineral cycling in aquatic macrophyte communities of the Chowan River, North Carolina. Water Resour. Res. Inst. Univ. North Carolina, Rpt. No. 120, Raleigh. 137 pp.
- Brown, W.H. 1913. The relation of the substratum to the growth of Elodea. Phillipine J. Sci. C. Botany 8:1-20.
- Bumby, M.J. 1977. Changes in submersed macrophytes in Green Lake, Wisconsin, from 1921 to 1971. Trans. Wisc. Acad. Arts Sci. Lett. 65:120-151.
- Butcher, R.W. 1933. Studies on the ecology of rivers. I. On the distribution of macrophytic vegetation in the rivers of Britain. J. Ecol. 21:58-91.
- Cahoon, W.G. 1953. Commercial carp removal at Lake Mattamuskeet, North Carolina. J. Wildl. Mgmt. 17:312-317.
- Cardone, A.J. and D.W. Kelley. 1961. The influences of inorganic sediment on the aquatic life of streams. Calif. Fish and Game 47:189-228.
- Carr, J.L. 1969a. The primary productivity and physiology of Ceratophyllum demersum. I. Gross macro primary productivity. Aust. J. Mar. Freshw. Res. 20:115-126.
- Carr, J.L. 1969b. The primary productivity and physiology of Ceratophyllum demersum. II. Micro primary productivity, pH, and P/R ratio. Aust. J. Mar. Freshw. Res. 20:127-142.
- Christensen, T. and F. Andersen. 1958. De større vandplanter i Furesø, Furesøunder-søgelse, 1950-1954. Folia Limnol. Scand. 10:114-128. (Cited in Hutchinson, 1975.)
- Cole, G.A. 1975. Textbook of Limnology. C.V. Mosby Co., St. Louis. 283 pp.
- Cole, G.A. and W.T. Barry. 1973. Montezuma Well, Arizona, as a habitat. J. Ariz. Acad. Sci. 8:7-13.
- Correll, D.L., J.W. Pierce, and T.L. Wu. 1978. Herbicides and submerged plants in Chesapeake Bay. In: Coastal Zone '78, 2:858-877.
- Craig, S.R. 1976. Seasonal development of structure in the macrophytic communities in Lake Opinicon, Ontario. M.S. Thesis, Queens Univ., Kingston, Ontario, Canada. 104 pp.
- Crowder, A.A., J.M. Bristow, M.R. King, and S. Vanderkloet. 1977. Distribution, seasonality, and biomass of aquatic macrophytes in Lake Opinicon (Eastern Ontario). Naturaliste Can. 104:441-456.

- Crum, G.H. and R.W. Bachmann. 1973. Submersed aquatic plants of the Iowa Great Lakes region. Iowa State J. Res. 48:147-173.
- Davis, G.J. and J.H. Steenis. 1973. Eurasian watermilfoil: Problems and proposed solutions. Friend O'Wildlife 16:4-5.
- Davis, G.J. and M.M. Brinson. 1976. The submersed macrophytes of the Pamlico River estuary, North Carolina. Water Resour. Res. Inst. Univ. North Carolina, Rpt. No. 112, Raleigh. 202 pp.
- Denniston, R.H. 1921. A survey of the larger aquatic plants of Lake Mendota. Trans. Wisc. Acad. Arts Sci. Lett. 20:495-500.
- Denny, P. 1972. Sites of nutrient absorption in aquatic macrophytes. J. Ecol. 60:819-829.
- Denny, P. 1973. Lakes of south-western Uganda. II. Vegetation studies on Lake Bunyonyi. Freshwater Biol. 3:123-135.
- Fassett, N.C. 1957. A Manual of Aquatic Plants. Univ. Wisconsin Press, Madison, 405 pp.
- Ferling, E. 1957. Die Wirkungen des Erhöhten hydrostatischen Druckes auf Wachstum und Differenzierung submerser Blütenpflanzen. Planta 49:235-270.
- Fernald, M.L. 1950. Gray's Manual of Botany. American Book Co., N.Y. 1632 pp.
- Gessner, F. 1938. Die Beziehung zwischen Lichtintensität und Assimilation bei submerser Wasserpflanzen. Jahrb. Wiss. Bot. 86:491-526.
- Gessner, F. 1952. Der Druck in seiner Bedeutung für das Wachstum submerser Wasserpflanzen. Planta 40:391-397.
- Golubic, S. 1963. Hydrostatischer Druck, Licht und submerser Vegetation im Vrana-See. Int. Revue ges. Hydrobiol. 48:1-7.
- Grace, J.B. and L.J. Tilly. 1976. Distribution and abundance of submerged macrophytes, including Myriophyllum spicatum L. (Angiospermae), in a reactor cooling reservoir. Arch. Hydrobiol. 77:475-487.
- Guilizzoni, P. 1977. Photosynthesis of the submergent macrophyte Ceratophyllum demersum in Lake Wingra. Wisc. Acad. Sci. Arts Lett. 65:152-161.
- Hartman, R.T. and D.L. Brown. 1967. Changes in internal atmosphere of submersed vascular hydrophytes in relation to photosynthesis. Ecology 48:252-258.
- Haslam, S.M. 1978. River Plants: The Macrophytic Vegetation of Watercourses. Cambridge Univ. Press, Cambridge, 396 pp.

- Hestand, R.S., B.E. May, D.P. Schultz, and C.R. Walker. 1973. Ecological implications of water levels on plant growth in a shallow reservoir. *Hyalanth Cont. J.* 11:54-58.
- Hjülstrom, F. 1935. Studies of the morphological activity of rivers as illustrated by the river Fyris. *Bull. Geol. Inst. Uppsala* 25:221-527.
- Holmes, R.W. 1970. The Secchi disk in turbid coastal waters. *Limnol. Oceanogr.* 15:688-694.
- Hunt, G.S. 1963. Wild celery in the lower Detroit River. *Ecology* 44:360-369.
- Hutchinson, G.E. 1957. *A Treatise on Limnology, Vol. I. Geography, Physics, and Chemistry.* John Wiley & Sons, New York. 1015 pp.
- Hutchinson, G.E. 1975. *A Treatise on Limnology, Vol. III: Limnological Botany.* John Wiley & Sons, New York. 660 pp.
- Hynes, H.B.N. 1970a. *The Ecology of Running Waters.* Univ. Toronto Press. 555 pp.
- Hynes, H.B.N. 1970b. The ecology of flowing waters. *Water Poll. Cont. J.* 42:418-424.
- Ikusima, I. 1965. Ecological studies on the productivity of aquatic plant communities. I. Measurement of photosynthetic activity. *Bot. Mag. Tokyo* 78:202-211.
- Ikusima, I. 1966. Ecological studies on the productivity of aquatic plant communities. II. Seasonal changes in standing crop and productivity of a natural submerged community of Vallisneria denseserrulata. *Bot. Mag. Tokyo* 79:7-19.
- Ikusima, I. 1967. Ecological studies on the productivity of aquatic plant communities. III. Effect of depth on daily photosynthesis in submerged macrophytes. *Bot. Mag. Tokyo* 80:57-67.
- James, H.R. and E.A. Birge. 1938. A laboratory study of the absorption of light by lake waters. *Trans. Wis. Acad. Sci. Arts Lett.* 31:1-154.
- Jackson, H.O. and W.C. Starrett. 1959. Turbidity and sedimentation at Lake Chautauqua, Illinois. *J. Wildl. Mgmt.* 14:157-168.
- Jimbo, T., M. Takamatsu, and H. Kuraishi. 1955. Notes on the aquatic vegetation of Lake Towada. *Ecol. Rev.* 14:1-9.
- Jupp, B.P., D.H.N. Spence, and R.H. Britton. 1974. The distribution and production of submersed macrophytes in Loch Leven, Kinross. *Proc. Roy. Soc. Edinb. B*, 74:195-208.

- Jupp, B.P. and D.H.N. Spence. 1977a. Limitations on macrophytes in a eutrophic lake, Loch Leven. I. Effects of phytoplankton. J. Ecol. 65:175-186.
- Jupp, B.P. and D.H.N. Spence. 1977b. Limitations of macrophytes in a eutrophic lake, Loch Leven. II. Wave action, sediments and waterfowl grazing. J. Ecol. 65:431-446.
- Krumbein, W.C. and L.L. Sloss. 1963. Stratigraphy and Sedimentation, 2nd edition. W.H. Freeman and Co., San Francisco. 660 pp.
- Lind, C.T. and G. Cottam. 1969. The submersed aquatics of University Bay: A study in eutrophication. Amer. Midl. Nat. 81:353-369.
- Lynch, J.J., T. O'Neil and D.W. Lag. 1947. Management significance of damage by geese and muskrats to Gulf Coast marshes. J. Wildl. Mgmt. 11:50-76.
- Martin, A.C. and F.M. Uhler. 1939. Food of game ducks in the United States and Canada. U.S.D.A. Tech. Bull. No. 634, Washington. 147 pp.
- McCombie, A.M. and I. Wile. 1971. Ecology of aquatic vascular plants in southern Ontario impoundments. Weed Sci. 19:225-228.
- McIntosh, A.W., B.K. Shephard, R.A. Mayes, G.J. Atchison, and D.W. Nelson. 1978. Some aspects of sediment distribution and macrophyte cycling of heavy metals in a contaminated lake. J. Environ. Qual. 7:301-305.
- Metcalf, F.P. 1931. Wild duck foods of North Dakota lakes. U.S. Dept. of Agriculture. Tech. Bull. No. 221. Washington. 71 pp.
- Meyer, B.S. and A.C. Heritage. 1941. Effect of turbidity and depth of immersion on apparent photosynthesis in Ceratophyllum demersum. Ecology 22:17-22.
- Meyer, B.S., F.H. Bell, L.C. Thompson, and E.I. Clay. 1943. Effect of depth of immersion on apparent photosynthesis in submersed vascular aquatics. Ecology 24:393-399.
- Misra, R.D. 1938. Edaphic factors in the distribution of aquatic plants in the English Lakes. J. Ecol. 26:411-451.
- Moeller, R.E. 1975. Hydrophyte biomass and community structure in a small oligotrophic New Hampshire lake. Verh. Inter. Verein. Limnol. 19:1004-1012.
- Morton, J.W. 1977. Ecological effects of dredging and dredge spoil disposal: a literature review. U.S. Fish and Wildlife Service Tech. Paper No. 94, Washington. 33 pp.
- Moyle, J.B. 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. Amer. Midl. Nat. 34:402-420.

- Nall, L.E. and J.D. Schardt. 1978. The aquatic macrophytes of Lake Conway, Florida. In: Large-Scale Operations Management Test of Use of the White Amur for Control of Problem Aquatic Plants; Report 1, Baseline Studies, Vol. I. U.S. Army Engineer District, Jacksonville, Fla. 118 pp.
- Nichols, S.A. 1975. The impact of overwinter drawdown on the aquatic vegetation of the Chippewa Flowage, Wisconsin. Wisc. Acad. Sci. Arts Lett. 63:176-185.
- Nichols, S.A. and S. Mori. 1971. The littoral macrophyte vegetation of Lake Wingra: An example of a Myriophyllum spicatum invasion in a southern Wisconsin Lake. Trans. Wisc. Acad. Arts Sci. Lett. 59:107-119.
- Nichols, D.S. and D.R. Keeney. 1976. Nitrogen nutrition of Myriophyllum spicatum: Uptake and translocation of ^{15}N by shoots and roots. Freshwater Biol. 6:145-154.
- Nicholson, S.A. and B.A. Aroyo. 1975. A case study in hydrarch zonation. Vegetatio 30:207-212.
- Odum, H.T. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1:102-117.
- Odum, H.T. 1963. Productivity measurements in Texas turtle grass and the effects of dredging an intracoastal channel. Univ. Texas, Inst. Mar. Sci. Publ. 9:48-58.
- Odum, H.T. 1971. Environment, Power, and Society. Wiley Interscience, N.Y. 331 pp.
- Oglesby, R.T., A. Vogel, J.H. Peverly, and R. Johnson. 1976. Changes in submerged plants at the south end of Cayuga Lake following Tropical Storm Agnes. Hydrobiologia 48:251-255.
- O'Rear, C.W., Jr. 1975. The effects of stream channelization on the distribution of nutrients and metals. Water Resour. Res. Inst. Univ. North Carolina, Rpt. No. 108, Raleigh. 52 pp.
- Otto, N.E. and P.F. Enger. 1960. Some effects of suspended sediment on growth of submersed pondweeds. Gen. Lab. Rep. No. Gen-27. U.S. Dept. Interior, Bureau of Reclamation, Denver, Colorado. 18 pp.
- Ozimek, T. 1978. Effect of municipal sewage on the submerged macrophytes of a lake littoral. Ecol. Pol. 26:3-39.
- Pearsall, W.H. 1920. The aquatic vegetation of English Lakes. J. Ecol. 8: 163-201.

- Pearsall, W.H. 1921. The development of vegetation in the English Lakes, considered in relation to the general evolution of glacial lakes and rock basins. *Proc. R. Soc. Lond.* 92B:259-284.
- Peltier, W.H. and E.B. Welch. 1969. Factors affecting growth of rooted aquatic plants in a river. *Weed Sci.* 17:412-416.
- Peltier, W.H. and E.B. Welch. 1970. Factors affecting growth of rooted aquatic plants in a reservoir. *Weed Sci.* 18:7-9.
- Phillips, G.L., D. Eminson, and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Bot.* 4:103-126.
- Pieters, A.J. 1901. The plants of western Lake Erie, with observations on their distribution. *Bull. U.S. Fish Comm.* 21:57-79 (cited in Stuckey, 1971).
- Pond, R.H. 1903. The biological relation of aquatic plants to the substratum. *Publ. U.S. Comm. of Fish and Fisheries. Rept. for 1903*, pp. 485-526.
- Poole, H.H. and W.R.G. Atkins. 1929. Photo-electric measurements of submarine illumination throughout the year. *J. Mar. Biol. Assoc., U.K.* 16: 297-324.
- Potzger, J.E. and W.A. Van Engel. 1942. Study of the rooted aquatic vegetation of Weber Lake, Vilas County, Wisconsin. *Trans. Wisc. Acad. Arts Sci. Lett.* 34:149-166.
- Rich, P.H., R.G. Wetzel, and N. Van Thuy. 1971. Distribution, production, and role of aquatic macrophytes in a southern Michigan marl lake. *Freshwater Biol.* 1:3-21.
- Rickett, H.W. 1922. A quantitative study of the larger aquatic plants of Lake Mendota. *Trans. Wisc. Acad. Arts Sci. Lett.* 20:501-527.
- Rickett, H.W. 1924. A quantitative study of the large aquatic plants of Green Lake, Wisconsin. *Trans. Wisc. Acad. Arts Sci. Lett.* 21:381-414.
- Schiemer, F. and M. Prosser. 1976. Distribution and biomass of submerged macrophytes in Neusiedlersee. *Aquatic Bot.* 2:289-307.
- Schmid, W.D. 1965. Distribution of aquatic vegetation as measured by line intercept with scuba. *Ecology* 46:816-823.
- Schulthrope, C.D. 1967. *The Biology of Aquatic Vascular Plants.* Edward Arnold Ltd., Lond. 610 pp.

- Seidelin Raunkiaer, A. and J. Boye Petersen. 1917. In: Wesenberg Lund, C., Sand, M.J., Boye Petersen, J., Weidilin Raunkiaer, A., and Steenberg, C. M., Furesøstudier. K. Dan Vidensk. Selsk. Skr. Nat. Mat. Afd., Rackke 8, 3, No. 1:58-77 (cited in Hutchinson, 1975).
- Sheldon, R.B. and C.W. Boylen. 1977. Maximum depth inhabited by aquatic vascular plants. *Amer. Midl. Nat.* 97:248-254.
- Shelter, S.G. and L.E. Skog. 1978. A Provisional Checklist of Species for North America (Revised). Missouri Botanical Garden, St. Louis. 199 pp.
- Sincock, J.L. 1965. Data Report - Back Bay, Virginia and Currituck Sound, North Carolina Cooperative Investigations. Patuxent Wildlife Research Center, Laurel, Maryland. 1600 pp.
- Sorensen, D.L., M.M. McCarthy, E.J. Middlebrooks, and D.B. Porcella. 1977. Suspended and dissolved solids effects on freshwater biota: A review. U.S. Environmental Agency, EPA-600/3-77-042, Corvallis. 64 pp.
- Spence, D.H.N. 1964. The macrophytic vegetation of freshwater lochs, swamps, and associated fens, pp. 306-425. In: J.H. Burnett (ed.), *The Vegetation of Scotland*. Oliver and Boyd, Edinburgh.
- Spence, D.H.N. 1967. Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. *J. Ecol.* 55:147-170.
- Spence, D.H.N. 1976. Light and plant response in fresh water, pp. 93-133. In: G.C. Evans, R. Bainbridge and O. Rackham (eds.), *Light as an Ecological Factor: II*. Blackwell Scientific Publications, Oxford.
- Spence, D.H.N. and J. Chrystal. 1970a. Photosynthesis and zonation of freshwater macrophytes. I. Depth distribution and shade tolerance. *New Phytol.* 69:205-215.
- Spence, D.H.N. and J. Chrystal. 1970b. Photosynthesis and zonation of freshwater macrophytes. II. Adaptability of species in deep and shallow waters. *New Phytol.* 69:217-227.
- Steenis, J.H. 1932. Lakes of Sawyer County. In: *Land Economic Inventory of Northern Wisconsin: Sawyer County*. Wisc. Dept. of Agri. and Markets Bull. No. 138. 58 pp.
- Steenis, J.H. 1947. Recent changes in the marsh and aquatic plant status at Reelfoot Lake. *J. Tenn. Acad. Sci.* 22:22-27.
- Steenis, J.H. 1970. Status of Eurasian watermilfoil and associated submerged species in the Chesapeake Bay area - 1969. Mimeo. Report, Patuxent Wildl. Research Cntr., Laurel, Maryland. 28 pp.

- Steenis, J.H., V.D. Stotts, and C.R. Gillette. 1962. Observations on distribution and control of Eurasian watermilfoil in Chesapeake Bay; 1961. Proc. 16th Ann. Meet. Northeast. Weed Cont. Conf. 16:442-448.
- Steenis, J.H., V.D. Stotts, and C.K. Rawls. 1971. Status of Eurasian watermilfoil and associated species in the Chesapeake Bay area, 1970 and 1971. Mimeo. Rept., Patuxent Wildlife Research Center. 13 pp.
- Stern, E.M. and W.B. Stickle. 1978. Effects of turbidity and suspended material in aquatic environments: Literature review. U.S. Army Corps of Engineers Tech. Rpt. D-78-21, Washington. 117 pp.
- Stuckey, R.L. 1971. Changes of vascular aquatic flowering plants during 70 years in Put-in-Bay Harbor, Lake Erie, Ohio. Ohio J. Sci. 71:321-342.
- Thorndale, T. 1898. Island Jottings. Sandusky Weekly Register 30 March: 11. (cited in Stuckey, 1971.)
- Thunmark, S. 1931. Dee See Fiolen und seine Vegetation. Acta. Phytogeogr. Suec. 2; 198 pp. (cited in Hutchinson, 1975).
- Tutin, T.G. 1940. The Percy Sladen Trust Expedition to Lake Titicaca in 1937 under the leadership of Mr. H. Cary Gilson, M.A. X. The macrophytic vegetation of the lake. Trans. Linn. Soc. Lond., 3rd Ser. 1:161-189.
- Twilley, R.R., M.M. Brinson, and G.J. Davis. 1977. Phosphorus absorption, translocation, and secretion in Nuphar luteum. Limnol. Oceanogr. 22:1022-1032.
- Van, T.K., W.T. Haller, and G. Bowes. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. Plant Physiol. 58:761-768.
- van der Valk, A.G. and C.B. Davis. 1976. Changes in the composition, structure, and production of plant communities along a perturbed wetland coenocline. Vegetatio 32:87-96.
- Verduin, J. 1956. Energy fixation and utilization by natural communities in western Lake Erie. Ecology 37:40-50.
- Volker, R. and S.G. Smith. 1965. Changes in aquatic vascular flora of Lake East Okoboji in historic times. Iowa Acad. Sci., Proc. 72:65-72.
- Weber, J.A. and L.D. Nooden. 1976a. Environmental and hormonal control of turion formation in Myriophyllum verticillatum. Plant Cell Physiol. 17: 721-731.
- Weber, J.A. and L.D. Nooden. 1976b. Environmental and hormonal control of turion germination in Myriophyllum verticillatum. Amer. J. Bot. 63:936-944.

- Westlake, D.F. 1966. The light climate for plants in rivers. Symp. British Ecol. Soc. 6:99-119.
- Westlake, D.F. 1967. Some effects of low-velocity currents on the metabolism of aquatic macrophytes. J. Expt. Bot. 18:187-205.
- Westlake, D.F. 1968. The biology of aquatic weeds in relation to their management. Proc. Ninth Brit. Weed Cont. Conf. pp. 372-381.
- Westlake, D.F. 1973. Aquatic macrophytes in rivers: A review. Pol. Arch. Hydrobiol. 20:31-40.
- Wetzel, R.G. 1975. Limnology. W.B. Saunders Co., Philadelphia. 743 pp.
- Wetzel, R.G. and R.A. Hough. 1973. Productivity and role of aquatic macrophytes in lakes. An assessment. Pol. Arch. Hydrobiol. 20:9-19.
- Wilson, L.R. 1935. Lake development and plant succession in Vilas County, Wisconsin. Part I. The medium hard water lakes. Ecol. Monogr. 5:207-247.
- Wilson, L.R. 1941. The larger aquatic vegetation of Trout Lake, Vilas County, Wisconsin. Trans. Wisc. Acad. Sci. Lett. 33:135-146.



Appendix A. Regions of North America that correspond to the distribution codes of the Appendix B.

Appendix B. Species, Family, Common Name, and Distribution of North American Aquatic Macrophytes Mentioned in Text. The Distribution Code Corresponds with Regions in Appendix A Adapted from Shelter and Skog (1978) Except as Indicated: (*) Fassett (1957) and (**) Fernald (1950)

Species	Family	Common Name	Distribution
<u>Alisma gramineum</u> var. <u>geyeri</u> J. G. Gmel.	Alismataceae	Narrowleaf Water Plantain	1,3,4,5,8,9,0
<u>Amoracia aquatica</u> (Eat.) Wieg.	Brassicaceae	Lake Cress	1,2,3,6,E
<u>Bidens beckii</u> J. Torrey	Asteraceae	Water Marigold	1,3,9,W,P,E,M
<u>Butomus umbellatus</u> f. <u>vallisnerifolius</u> L.	Butomaceae	Flowering Rush	1,3,9,P,E,M
<u>Cambomba caroliniana</u> A. Gray	Nymphaeaceae	Fanwort	1,2,3,6
<u>Ceratophyllum demersum</u> L.	Ceratophyllaceae	Coontail, Hornwort	1,2,3,4,5,6,7,8,9 0,A,H,C,N,P,E,M
<u>Cyperus esculentus</u> L.	Cyperaceae	Nut Grass, Ground Almond	1,2,3,4,5,6,7,8,9 0,A,E,M
<u>Elatine minima</u> (Nutt.) F. E. L. Fischer and C.A. Meyer	Elatinaceae	Waterwort	1,3,E,M
<u>Eleocharis acicularis</u> (L.) J. J. Roem. and Schult.	Cyperaceae	Slender Spikerush	1,2,3,4,5,6,7,8,9 0,A,N,W,P,E,M,G
<u>Eleocharis parvula</u> (J. J. Roem. and Schult.) Link	Cyperaceae	Dwarf Spikerush	1,2,3,4,5,6,7,8,9,0 W,E,M

Continued

Appendix B (Continued)

Species	Family	Common Name	Distribution
<u>Elodea canadensis</u> Michx.	Hydrocharitaceae	Waterweed	1,2,3,4,5,6,7,8,9 0,W,P,E,M
<u>Elodea nuttallii</u> (Planch.) H. St. John	Hydrocharitaceae	Waterweed	1,3,4,5,8,9,0,E,M
<u>Eriocaulon septangulare</u> With.	Eriocaulaceae	Pipewort	1,2,3,6,E,M
<u>Gratiola aurea</u> Pursch	Scrophulariaceae	Hedge Hyssop, Goldenpert	1,2,3,4,5,E,M
<u>Gratiola lutea</u> f. <u>pusilla</u> (Fassett) Pennell.	Scrophulariaceae	Dwarf Hyssop	1,3,E,M*
<u>Heteranthera dubia</u> (Jacq.) MacMill.	Pontederiaceae	Water Stargrass	1,2,3,4,5,6,7,8,9 0,E
<u>Hydrilla verticillata</u> Royle	Hydrocharitaceae	Hydrilla	2
<u>Isoetes macrospora</u> Durieu	Isoetaceae	Quillwort	1,3,E,M
<u>Juncus pelocarpus</u> E. Meyer	Juncaceae	Bog Rush	1,2,3,E,M
<u>Littorella americana</u> Fern.	Plantaginaceae		1,2,3,E,M
<u>Lobelia dortmanna</u> L.	Campanulaceae	Water Lobelia	1,3,4,9,W,P,E,M
<u>Myriophyllum alterniflorum</u> DC.	Haloragaceae	Little Watermil- foil	1,A,N,P,E,M,G

Continued

Appendix B (Continued)

Species	Family	Common Name	Distribution
<u>Myriophyllum exallescens</u> Fern.	Haloragaceae	Northern Watermill-foil	1,2,3,4,5,6,8,9,0 A,N,W,P,E,M,G*
<u>Myriophyllum heterophyllum</u> Michx.	Haloragaceae	Variable Watermill-foil	1,2,3,4,5,6,E
<u>Myriophyllum spicatum</u> L.	Haloragaceae	Eurasian Watermill-foil	1,2,3,4,5,6,8,9,0 A,N,W,P,E,M,G
<u>Myriophyllum tenellum</u> Bigel.	Haloragaceae	Leafless Watermill-foil	1,3,E,M
<u>Myriophyllum verticillatum</u> L.	Haloragaceae	Whorled Watermillfoil	1,2,3,4,5,8,9,0,A
<u>Najas flexilis</u> (Willd.) Rostk. and Schmidt	Najadaceae	Northern Naiad, Bushy Pondweed	1,2,3,4,5,7,8,9,W P,E,M
<u>Najas guadalupensis</u> (Spreng.) Magnus	Najadaceae	Southern Naiad, Bushy Pondweed	1,2,3,4,5,6,7,8,9 0,E
<u>Najas minor</u> All.	Najadaceae	Bushy Pondweed, Naiad	1,2,3
<u>Potamogeton amplifolius</u> Tuckerm.	Potamogetonaceae	Largeleaf Pondweed	1,2,3,4,5,7,8,9,0 W,P,E,M
<u>Potamogeton berchtoldii</u> Fieber	Potamogetonaceae	Slender Pondweed	1,2,3,4,5,6,8,9,0 A,N,W,P,E,M,G**

Continued

Appendix B (Continued)

Species	Family	Common Name	Distribution
<u>Potamogeton crispus</u> L.	Potamogetonaceae	Muck Pondweed, Curly Pondweed	1,2,3,4,5,6,8,9 0,E,M
<u>Potamogeton diversifolius</u> Raf.	Potamogetonaceae	Snailseed Pondweed	1,2,3,4,5,6,7,8,9, 0
<u>Potamogeton epihydrus</u> Raf.	Potamogetonaceae	Ribbonleaf Pondweed	1,2,3,4,5,8,9,0 A,W,P,E,M
<u>Potamogeton filiformis</u> Pers.	Potamogetonaceae	Threadleaf Pondweed	1,3,4,5,8,9,0,A
<u>Potamogeton foliosus</u> Raf.	Potamogetonaceae	Leafy Pondweed	1,2,3,4,5,6,7,8,9, 0,A,N,W,P,E,M
<u>Potamogeton friesii</u> Rupr.	Potamogetonaceae	Fries Pondweed	1,3,4,8,9,A,N,W,P, E,M
<u>Potamogeton gramineus</u> L.	Potamogetonaceae	Variableleaf Pond- weed	1,3,4,5,7,8,9,0 A,N,W,P,E,M,G
<u>Potamogeton illinoensis</u> Morong.	Potamogetonaceae	Variableleaf Pond- weed	1,2,3,4,5,6,7,8,9 0,A,W,P,E,M
<u>Potamogeton lucens</u> L.	Potamogetonaceae	Variableleaf Pond- weed	1,2,3,4,5,6,7,8,9 0,A,W,P,E,M
<u>Potamogeton natans</u> L.	Potamogetonaceae	Floatingleaf Pond- weed	1,2,3,4,5,6,7,8,9 0,A,W,P,E,M,G

Continued

Appendix B (Continued)

Species	Family	Common Name	Distribution
<u>Potamogeton nodosus</u> Poir.	Potamogetonaceae	Longleaf Pondweed	1,2,3,4,5,6,7,8,9 O,W,E,M
<u>Potamogeton obtusifolius</u> F. C. Mert. and W. C. J. Koch	Potamogetonaceae	Bluntleaf Pondweed	1,3,4,5,W,P,E,M
<u>Potamogeton pectinatus</u> L.	Potamogetonaceae	Sago Pondweed	1,2,3,4,5,6,7,8,9 O,A,N,W,P,E,M
<u>Potamogeton</u> subsection <u>Perfoliati</u> (Includes <u>P. perfoliatus</u> L., <u>P.</u> <u>perfoliatus</u> var. <u>bupleuroides</u> (Fern.) Fairw., and <u>P. richardsonii</u> (Ar. Benn.) Rybd.	Potamogetonaceae	Redhead Grass, Claspingleaf Pondweed	1,2,3,4,5,A,N,E,M G
<u>Potamogeton praelongus</u> F. Wulf.	Potamogetonaceae	Whitestream Pond- weed	1,3,4,5,7,8,9,0 A,N,W,P,E,M,G
<u>Potamogeton pusillus</u> L.	Potamogetonaceae	Slender Pondweed	1,2,3,4,5,6,7,8,9 O,A,N,W,P,E,M,G
<u>Potamogeton robbinsii</u> Oakes	Potamogetonaceae	Fernleaf Pondweed	1,3,4,8,9,0,A,W,P E,M
<u>Potamogeton spirillus</u> Tuckerm.	Potamogetonaceae	Snailseed Pondweed	1,3,4,E,M
<u>Potamogeton strictifolius</u> Benn.	Potamogetonaceae	Pondweed	1,3,4,5,8,9
<u>Potamogeton zosteriformis</u> Fern.	Potamogetonaceae	Flatstem Pondweed	1,3,4,5,8,9,0,A,M W,P,E,M

Continued

Appendix B (Continued)

Species	Family	Common Name	Distribution
<u>Proserpinaca palustris</u> L.	Haloragaceae	Mermaid Weed	1,2,3,6,0,E,M
<u>Ranunculus aquatilis</u> L.	Ranunculaceae	White Water Buttercup, Growfoot	1,3,4,5,7,8,9,0,A,N,W,P,E,M,G
<u>Ranunculus longirostris</u> Godron.	Ranunculaceae	White Water Buttercup	1,3,5,6,7,E*
<u>Ruppia maritima</u> L.	Potamogetonaceae	Widgeon Grass	1,2,3,4,5,6,8,9,)A,W,P,E,M
<u>Sagittaria cuneata</u> Sheld.	Alismataceae	Northern Arrowhead, Duckpotato	1,3,4,5,7,8,9,0,A,N,W,P,E,M
<u>Sagittaria graminea</u> Michx.	Alismataceae	Slender Arrowhead	1,2,3,4,5,6,7,E,M
<u>Sagittaria subulata</u> (L.) Buckl.	Alismataceae	Water Arrowhead	1,2,9
<u>Scirpus acutus</u> Muhl.	Cyperaceae	Hardstem Bulrush	1,2,3,4,5,6,7,8,90
<u>Scirpus subterminalis</u> J. Torr.	Cyperaceae	Water Bulrush	1,2,3,4,9,A,W,E,M
<u>Sparganium angustifolium</u> Michx.	Sparganiaceae	Burreed	1,3,4,7,8,9,0,A,N,W,P,E,M,G
<u>Subularia aquatica</u> L.	Brassicaceae	Awlwort	1,3,4,8,9,0,A,N,W,P,E,M,G

(continued)

Appendix B (Concluded)

Species	Family	Common Name	Distribution
<u>Utricularia cornuta</u> Michx.	Lentibulariaceae	Horned Bladderwort	1,2,3,6,0,P,E,M
<u>Utricularia gibba</u> L.	Lentibulariaceae	Eastern Bladderwort	1,2,3,5,6,0,C,E,M
<u>Utricularia intermedia</u> Hayne	Lentibulariaceae	Flatleaf Bladderwort	1,3,4,8,9,0,A,N,W P,E,M,G
<u>Utricularia minor</u> L.	Lentibulariaceae	Purple Bladderwort	1,2,3,E,M
<u>Utricularia resupinata</u> B. D. Greene	Lentibulariaceae	Lavender Bladderwort	1,2,3,E,M
<u>Utricularia vulgaris</u> L.	Lentibulariaceae	Common Bladderwort	1,2,3,4,5,6,7,8,9 0,A,N,W,P,E,M
<u>Vallisneria americana</u> Michx.	Hydrocharitaceae	Wildcelery	1,2,4
<u>Zannichellia palustris</u> L.	Zannichelliaceae	Horned Pondweed	1,2,3,4,5,6,7,8,9 0,A,N,W,P,E,M
<u>Zostera marina</u> L.	Potamogetonaceae	Eelgrass	1,2,9,0,A,N,W,P,E M,G

50272-101

REPORT DOCUMENTATION PAGE	1. REPORT NO. FWS/OBS-79/33	2.	3. Recipient's Accession No.
4. Title and Subtitle Responses of Submersed Vascular Plant Communities to Environmental Change		5. Report Date August 1980	
7. Author(s) Davis, Graham J., and Brinson, Mark M.		6.	
9. Performing Organization Name and Address Department of Biology East Carolina University Greenville, NC 27834		8. Performing Organization Rept. No.	
12. Sponsoring Organization Name and Address Eastern Energy and Land Use Team, Office of Biological Services, Fish and Wildlife Service, U. S. Department of the Interior Route 3 Box 44, Kearneysville, West Virginia 25430		10. Project/Task/Work Unit No.	
		11. Contract(C) or Grant(G) No. (C) 14-16-0009-78-032 (G)	
		13. Type of Report & Period Covered Final report	
15. Supplementary Notes		14.	
16. Abstract (Limit: 200 words)			
<p>This report examines the response of submersed vascular plants to changing environmental conditions, primarily those that affect light transmission. Among the physical factors considered are fluctuating water levels, currents and waves, and suspended sediments. Chemical and biological factors affecting plant responses to light conditions are growing season and dormancy, nutrient availability, and plant-animal interactions. Depth distribution data for many North American species of submersed vascular macrophytes are recorded as an indices of resistance to turbidity for some of the most tolerant of the species. Survival indices were also calculated for several species typically found in clearwater lakes. Turbidity tolerance and survival indices were then used to identify groups of species with varying degrees of resistance to ecosystem alterations. The report concludes with a brief discussion of the potential effects of human activities on submersed plant communities.</p> <p>There is a companion document which contains a summary of this literature review. It is entitled Responses of Submersed Vascular Plant Communities to Environmental Changes: Summary, FWS/OBS-80/42, August 1980.</p>			
17. Document Analysis			
a. Descriptors Aquatic Plants, Aquatic Environments, Light Penetration, Light Intensity, Water Level Fluctuations, Suspended Solids, Waves, Currents			
b. Identifiers/Open-Ended Terms Submersed Vascular plants, Aquatic Macrophytes, Light Transmissivity, Turbidity, Suspended Sediment			
c. COSATI Field/Group 43F, 48G, 57H			
18. Availability Statement Release unlimited		19. Security Class (This Report) Unclassified	21. No. of Pages 79
		20. Security Class (This Page) Unclassified	22. Price

(See ANSI-Z39.18)

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.



U. S. DEPARTMENT OF THE INTERIOR

**FISH AND WILDLIFE SERVICE
OFFICE OF BIOLOGICAL SERVICES
EASTERN ENERGY AND LAND USE TEAM
ROUTE 3, BOX 44
KEARNEYSVILLE, WV 25430**

**OFFICIAL BUSINESS
PENALTY FOR PRIVATE USE, \$300**

**POSTAGE AND FEES PAID
U S DEPARTMENT OF THE INTERIOR
INT-423**

