Biomass and distribution of submerged macrophytes in lakes

by

Carlos M. Duarte

A thesis presented to the Faculty of Graduate Studies and Research, McGill University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Department of Biology
McGill University
Montreal, Canada

May 1987

Ph. D. Biology

Carlos M. Duarte

Biomass and distribution of submerged macrophytes in lakes

ABSTRACT

The area covered by submerged macrophytes in any lake is a function of the underwater light regime. Biomass variability within a lake can be explained by differences in the slope of the littoral, whereas differences among lakes are best explained by both the slope and the water chemistry. Nutrient limitation of submerged biomass is most important in shallow littoral areas exposed to ice scouring early in spring and to wave action in the summer, whereas the deeper growing biomass appears to be most influenced by light and wave exposure.

RESUMÉ

La superficies couverte par les macrophytes submergés dans les lacs est fonction du régime d'illumination sous la surface de l'eau. La distribution de la biomasse est reliée à la pente de la zone littorale pour un lac donné, mais les différences entre les lacs sont mieux décrites en tenant compte également de la composition chimique de l'eau. Les éléments nutritifs limitent la biomasse des macrophytes submergés dans la partie supérieure du littoral sujette à l'abrasion par les glaces au printempts, et à l'action des vagues en été. La biomasse en eau plus profonde semble principalement reliée à la pénetration de la lumière et à l'exposition aux vagues.

CONTENTS

LIST OF TABLES

<u>Chapter 1.</u>

<u>Chapter 2</u>.

Chapter 3

Chapter 4

LIST OF FIGURES

PREFACE

The thesis is presented as a series of four related papers in publication format as permitted under the regulations of the Graduate Faculty of McGill University. All the papers are coauthored by my supervisor, Dr. J. Kalff, so that plural form "we" is used throughout the thesis. Chapter 1 is also coauthored by Dr. R. H. Peters, who contributed to the initial idea through discussions and whose criticisms improved the different manuscript versions of the chapter. Because these chapters are now published (Chapter I: Can. J. Fish. Aquat. Sci. 43: 1900-1908; Chapter II: Limnol. Oceanogr.31: 1072-1080) or submitted for publication (Chapters III and IV), some of the introduction and discussion of the different chapters is somewhat repetitive.

Faculty regulations require that the following statement on the elements of the thesis that are considered to be a contribution to original knowledge be included. These elements are:

(1) Equations allowing the prediction of the cover and biomass of submerged and emergent macrophytes in lakes from simple morphometric and climatic data.

(2) Demonstration of the strong relationship between submerged macrophyte biomass and littoral morphometry, and the use of this relationship predictively.

(3) Quantification of the contribution of littoral morphometry and water characteristics to explain the variability of submerged biomass in lakes, and examination of the relative contributions at different scales.

(4) Demonstration of the link between sediment nutrients and submerged biomass through the first *in situ* fertilization of natural macrophyte communities in lakes.

ACKNOWLEDGEMENTS

This thesis is the result of my education as a scientist. It is, therefore, not simply a personal achievement, but is the product of the efforts and interest of many people whom I wish to thank. I am grateful to Dolores Planas for introducing me to limnology, and to Jacob Kalff (my supervisor) for constant advice and support. I would also like to thank the World University Service of Canada for a scholarship, which financially supported the thesis and provided me the opportunity to be exposed to Canada in all its different aspects.

All members of the Limnology Researcg Centre of McGill University need to be acknowledged for contributing to the unique scientific atmosphere that greatly aided the development of the thesis through encouragement and the constructive criticisms received. I would like to thank in particular David Bird, Robert H. Peters, Yves Prairie and Joseph Rasmussen. I also want to acknowledge the field assistance provided by Anne-Marie L'Heureux, Leslie Pope, and Lucie Robidoux.

Very especially I would like to thank my immediate family for constant encouragement and support and for fully sharing the demands involved in the development of this thesis.

GENERAL INTRODUCTION

The study of lakes has been facilitated by their partition into two components, the pelagic zone and the littoral zone. These two zones differ, by definition, in the presence of macrophytic vegetation in the littoral zone and its absence in the pelagic zone (eg. Ruttner 1953, Welch 1952). This definition of the littoral zone identifies aquatic macrophytes as the most conspicuous, and perhaps most important, biological constituents. The physical extent of the influence of aquatic macrophytes on their environment depends on the area they cover, whereas the intensity of these influences appears to be a function of their biomass (eg. Canfield et al. 1983, Smith and Adams 1987).

Submerged macrophytes influence the biological and physico-chemical characteristics of the littoral zone in different ways: (1) they are important sources of new production to the ecosystem (Hutchinson 1975), (2) they influence phytoplankton biomass and production by trapping nutrients and shading the planktonic algae (Goulder 1969, Canfield et al. 1983), (3) their surfaces provide support for epiphytic algae (Cattaneo and Kalff 1979), which are important components of the diet of littoral invertebrates and fish (Sozska 1975), and (4) they introduce physical heterogeneity into the littoral zone of lakes and provide nesting sites and refuge from predation for fish (Wiley et al. 1984).

A quantification of the factors that influence the biomass of submerged macrophytes will, therefore, provide valuable knowledge of the environmental influence on the littoral zone as a whole. Nevertheless, the relative importance of different environmental constraints on the biomass of macrophytes is unknown (eg. Barko et al.

1986), and the factors controlling macrophyte cover are incompletely understood.

Laboratory studies of aquatic macrophyte growth have identified light intensity and temperature (eg. Barko and Smart 1981, Ikusima 1965), sediment characteristics (eg. Langeland 1982, Barko and Smart 1986), and inorganic carbon (eg. Black et al. 1981) as potential determinants of plant biomass. In addition, the influence of sediment nutrients (Anderson 1985), sediment granulometry (Chambers and Kalff 1985), wave action (Jupp and Spence 1977) and light intensity (Chambers and Kalff 1985) have been examined in a limited number of field experiments. Although laboratory studies can demonstrate the plausibility of some mechanisms of macrophyte biomass control they cannot establish their relative role in the field, because only a few of the factors involved can be studied simultaneously. Instead, correlational analysis based on field data may prove more useful to establish the relative importance of some factors to the determination of macrophyte biomass in lakes (eg. Anderson 1978).

I began by describing the association between the cover and biomass of emergent and submerged macrophytes on the one hand, and global climatic and physical characteristics of the lakes on the other (Chapter I). This analysis did not consider the variability in macrophyte biomass within lakes nor the important roles postulated for water characteristics in determining submerged biomass (eg. Hutchinson 1975, Wetzel and Grace 1983).

It is possible that the variability in submerged macrophytes within a lake stems from the diversity of sediment and physical conditions found there. Given the considerable variability of submerged biomass within lakes (eg. Nichols 1982), it is possible that the factors that generate within-lake variability (i.e. sediment and physical conditions) are as important as water characteristics. Since water properties remain relatively constant within a lake, they should be more important contributors to the between-lakes differences than to the within-lakes differences in macrophyte biomass. These hypotheses were tested by first identifying the components of the within-lake habitat heterogeneity that best explain the variability in macrophyte biomass (Chapter II), and then comparing their importance relative to water characteristics in a study of the variability in submerged biomass in a number of lakes ranging widely in both habitat heterogeneity and water characteristics (Chapter III).

To draw trustworthy conclusions from the above correlational studies require that the independent variables measured accurately reflect the factors they are supposed to represent. Whereas this is possible for most of these factors, accurately measuring the fraction of the sediment nutrients available for plant growth appears to be a difficult task (eg. Carignan 1982). Consequently, the weak relationship between submerged biomass and sediment nutrient concentrations often reported (eg. Anderson 1978, Langeland 1982, Anderson 1985) may simply be a consequence of the difficulties in measuring sediment nutrients. ALternatively, it may be that the strong influence of the littoral morphometry and the associated wave exposure upon both submerged macrophytes and sediment conditons masks the relationship between sediment nutrients and submerged biomass. To answer these questions I examined the growth response of submerged macrophytes to direct sediment fertilization and the effect of the physical conditions of the littoral zone on this response (Chapter IV).

REFERENCES

Anderson, M.G. 1978. Distribution and production of Sago Pondweed (Potamogeton pectinatus L.) on a northern prairie marsh. Ecology 59: 154-160.

Anderson, M.R. 1985. The relationship between sediment nutrient and aquatic macrophyte biomass in situ. Ph.D. thesis, McGill Univ. 153 pp.

Barko, J.W., and R.M. Smart. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. Ecol. Monogr. 51: 219-235.

______ , and ________ . 1986. Sediment-related mechanisms ofgroeth limitation in submersed macrophytes. Ecol. 67: 1328-1340.

______ , M.S. Adams, and N.L. Clesceri. 1986. Environmental factors and their consideration in the management of submerged aquatic vegetation: A review. J. Aquat. Plant Manage. 24: 1-10.

Black, M.A., S.C. Maberly, and D.H.N. Spence. 1981. Resistance to carbon dioxide fixation in four submerged freshwater macrophytes. New Phytol. 89: 557-568.

Canfield, D.E.,Jr., K.A. Langeland, M.J. Maceina, W.T. Haller, and J.V. Shireman. 1983a. Trophic state classification of lakes with aquatic macrophytes. Can. J. Fish. Aquat. Sci. 40: 1713-1718.

Cattaneo, A., and J. Kalff. 1979. Primary production of algae growing on natural and artificial aquatic plants: a study of interactions between epiphytes and their substrate. Limnol. Oceanogr. 24: 1031-1037.

Chambers, P.A., and J. Kalff. 1985. The influence of sediment composition and irradiance on the growth and morphology of Myriophyllum spicatum L. Aquat. Bot. 22: 253-263.

Goulder, R. 1969. Interactions between the rate of production of freshwater macrophytes and phytoplankton in a pond. Oikos 20: 300-309.

Hutchinson, G.E. 1975. A treatise on limnology. 3. Limnological botany. Wiley.

Ikusima, I. 1965. Ecological studies on the production of aquatic plant communities. 1. Measurement of photosynthetic activity. Bot. Mag., Tokyo 78: 202-211.

Jupp, B.P., and Spence, D.H.N. 1977. Limitations of macrophytes in a eutrophic lake, Loch Leven. II. Wave action, sediments and waterfowl grazing. J. Ecol. 65: 431-446.

Langeland, K.A., D.L. Sutton, and D.E. Canfield. 1983. Growth responses of Hydrilla verticilllata to extractable nuytrients in prepared substrates. J. Freshwat. Biol. 2: 263-272.

Nichols, S.A. 1982. Sampling characteristics of macrophyte biomass. Water Res. Bull. 18: 521-523.

Ruttner, F. 1953. Fundamentals of limnology. Univ. Toronto.

Smith, C.S., and M.S. Adams. Phosphorus transfer from sediments by Myriophyllum spicatum. Limnol. Oceanogr. 31: 1312-1321.

Sozska, G.J. 1975. Ecological relations between invertebrates and submersed macrophytes in the lake littoral. Ekol. Pol. 23: 393-415.

Welch, P.S. 1952. Limnology. McGraw Hill.

Wetzel, R.G., and J.B. Grace. 1983. Aquatic plant communities. pp. 223-290. In: E.R. Lemond (ed.), CO_2 and plants. AAAS selected symposiums series. Westview Press.

Wiley, J.L., R.W. Gorden, S.W. Waite, and T. Pwless. 1984. The relationship between aquatic macrophytes and fish production in Illinois ponds: a simple model. N. Am. J. Fish. Manage. 4: 111-119.

CHAPTER I

Patterns in biomass and cover of aquatic macrophytes in lakes

ABSTRACT

A quantitative analysis of biomass and cover of both submerged and emergent macrophytes in 139 lakes reported in the literature revealed that biomass and cover of emergent macrophytes are, on average, proportional to the lake area, but that the biomass and cover of submerged plants is proportionally reduced with increasing lake size. Underwater light was found to be the best descriptor of the cover and biomass of submerged plants. Conversely, emergent macrophytes are most strongly affected by lake morphometry, and in particular by its average slope. The predictability of the abundance of emergent and submerged macrophytes from these environmental factors stresses the predominant role that they play in macrophyte ecology and confirms the existence of strong patterns in the abundance of aquatic plants worldwide.

INTRODUCTION

Abundance of submerged macrophytes in lakes has been the subject of many regional studies (see Magnin 1893, Pearsall 1920, Maristo 1941, Spence 1967). These and other studies (reviewed by Hutchinson 1975) suggest a large number of factors that could bring about the wide variation in macrophyte cover and biomass in lakes. Unfortunately, these regional studies were not designed to assess quantitatively the relative influence of each of the proposed factors on the cover and biomass of aquatic macrophytes. Data have now become available to allow a quantitative assessment of the influence of environmental factors on the abundance of lake macrophytes.

We base this assessment on two community attributes: the surface area of lakes covered by submerged and emergent macrophytes and the total biomass of these plants. Surface area covered and biomass reflect different aspects of the ways macrophytes affect their environment. Macrophyte cover influences the littoral phytoplankton and zooplankton (Hasler and Jones 1949, Goulder 1969), epiphytes (Cattaneo and Kalff 1979), littoral invertebrates (Soszca 1975) and the abundance and composition of fish (Wiley et al. 1984, Whitfield 1984). In contrast, macrophyte biomass is more closely linked to ecosystem processes such as nutrient dynamics (Carpenter 1983, Canfield et al. 1983) and O_2 balance (Buscemi 1958, Edwards 1978).

Previous research identified light availability (Spence 1975, Chambers and Kalff 1985, Canfield et al. 1985), substrate characteristics (Pearsall 1920), lake trophic status (Hutchinson 1975) and lake morphometry (Pearsall 1917, Spence 1982, Duarte and Kalff 1986) as the most important nature.

It is presently presumed that oligotrophic lakes tend to have lower macrophyte biomass and cover than more productive ones (e.g. Hutchinson 1975), implying that increases in lake productivity should result in higher macrophyte abundance. However, this increase should also result in decreased light penetration in the water (e.g. Canfield et al. 1983), and subsequently, in the reduction of macrophyte cover (Phillips et al. 1978, Canfield et al. 1985). Consequently, although there is general agreement about the nature of the dominant factors influencing macrophyte cover and biomass, the effect of simultaneous changes in these variables remains unclear. Therefore, we examined available data on macrophyte cover and biomass to (1) gather empirical evidence for the relative importance of the major factors on the distribution and biomass of lake macrophytes, and (2) to develop preliminary models to predict macrophyte distribution and biomass under a wide variety of conditions.

Macrophyte characteristics

Data on macrophyte biomass and cover were obtained from the literature[1]. Macrophyte biomass is expressed in metric tons of dry weight. When other units were reported, biomass was transformed to dry weight by assuming dry weight to be 10% of fresh weight (Westlake 1965), ash free dry weight to be 80% of dry weight and organic carbon to be 37% of dry weight (Westlake 1974). In the two cases (Lakes Marion and Kalgaard) where only productivity values were provided for submerged macrophytes, biomass was assumed to correspond to 2/3 of production (Rich et al. 1971). Surface area covered by macrophytes is expressed in hectares. When only vegetation maps were provided, macrophyte cover was determine by planimetry, using a Hi-Pad digitizer (Houston Instruments).

Environmental variable selection

Light availability, sediment characteristics, lake trophy and lake morphometry are believed to be the major determinants of macrophyte cover and biomass. However, no single paper contains measures of all the environmental data needed for a given lake. We, therefore, used an estimate of the underwater light climate to reflect both photosynthetically available radiation and lake trophy. The underwater light climate is partially a function of geographic location of the lake, because location determines both the incident radiation and whether it is reduced by a winter ice cover. Lake trophic status and water color in turn determine light extinction in the water column. The annual irradiance at the lake

1. A complete data set and rteference list are available, at a nominal cost, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2.

surface (I_a, kcal cm^{-2} yr^{-1}) was obtained from climatic maps (Landsberg et al. 1966). Incoming irradiance penetrates open water and ice differently. Therefore, a correction for this is necessary. When the length of ice cover in days (Lic) was not specified, we used the equation developed by Shuter et al. (1983):

$$\ln(Lic) = 360 - 0.06\ T + 0.073\ \ln(Z) + 5.0$$

where T is the mean annual temperature (C) and Z is the mean depth of the lake (m). The mean annual temperature was calculated from the equation (Straskraba 1980):

$$T = 25.9 + 4.89\ 10^{-1}\ Lat' - 2.74\ 10^{-2}\ Lat'^{2} + 1.78\ 10^{-4}\ Lat'^{3}$$

When only the maximum depth of the lake was available, the mean depth of the lake was calculated from an equation we developed for lakes for which both were reported:

$$Z = 0.4\ \ Zmax - 0.54$$

$$R^2 = 0.89;\ N = 102,\ P<0.0001$$

This estimation of mean depth was used only to calculate the length of ice cover. Once the Lic was estimated, we took the average reflectances of an ice cover surface and open water to be 90% and 10% respectively (Margalef 1984). Consequently, the total irradiance just under the water surface (Io) can be approximated as:

$$Io = 0.9\ Is + 0.1\ Ii$$

where Is is the irradiance during the ice free season and Ii that reaching the ice covered lake; 0.9 and 0.1 represent the proportion of incident light which is not reflected by water and ice, respectively. The irradiance reaching the lake while ice covered (Ii) and ice free (Is) were obtained from the total annual irradiance (Ia) and the calculated length of the ice cover (Lic; Shuter et al. 1983), assuming that 1/3 of the Lic occurs before the winter solstice and 2/3 thereafter. The relation describing the percentage of the annual irradiance (%I = 100*Ii/Ia) received on each Julian day (D) at different latitudes (Lat) was developed from data in the Smithsonian tables (Smithsonian Institute 1939):

$$\%I = 19.3 + 26\ 10^{-4}\ D^2 - 0.24\ Lat - 15\ 10^{-4}\ Lat^2$$

$$R^2 = 0.96;\quad N=120;\quad P < 0.0001$$

The equation was used with the value of Ia for each lake to calculate Is, Ii and finally Io.

Additional climatic information such as the mean annual precipitation (P, in mm yr^{-1}) was obtained from a hydrological atlas (Kouzoun et al. 1977).

The proportion of the surface irradiance available to submerged macrophytes depends on the depths at which the plants grow and the absorption of light in the water column. To represent this, we developed composite variables to describe an average underwater irradiance. The amount I_o remaining at depth z in the water column (I_z) depends on the coefficient of attenuation, k, as defined by the Beer-Lambert law:

$$I_z = I_o\ e^{-kz}$$

The irradiance received by rooted plants is dependent on the irradiance received at the lake bottom. This was estimated by calculating the annual irradiance received down to the mean depth of the lake (I_z). However, as macrophytes grow towards the lake surface they depend more on the average light intensity in the water column (Iz) than on the light received at the bottom. The average irradiance within the mean depth of the lake was calculated using Riley's (1957) integration of the Beer-Lambert law:

$$Iz = Io\ (1 - e^{-k*z})/(k*z)$$

When k was not provided, it was approximated from the mean summer Secchi depth (Sd, m) assuming k= 1.46/Sd (Walker 1982). Mean summer Secchi depth was obtained from the same source as the macrophyte data or from the literature there mentioned, but only if the measurements were made within 1 year of the macrophyte survey. Water colour (as mg Pt/l) for the Finnish lakes in the data set was transformed to Secchi depth by using the equation developed by Eloranta (1978):

$$Sd = 17.54\ Colour^{-0.57}$$

These calculations idealize the lake as a straight sided water body with the same surface as the real lake but with a constant depth, Z. The two variables representing underwater irradiance ($\bar{I}_{\bar{Z}}$ and $I_{\bar{Z}}$) reflect the major factors affecting the underwater light climate by combining the theoretical effects of lake morphometry (Z), trophic status and water colour (through the attenuation coefficients, k) and geographical position (through its effect on the surface irradiance) into single variables.

Since sediment characteristics and wave action depend on lake morphometry (Hakanson 1981), we used morphometric factors as indexes of the sediment type and the energy environment of the littoral zone. Lake area (A, ha) was used to scale the lakes with respect to their total cover and biomass of submerged plants and as an index of wave action. The steepness of the lake basin was characterized by the index: $S = \sqrt{A}/\bar{Z}$ (Hakanson 1981), and the shape of the basin represented by the ratio of mean to maximum depth ($\bar{Z} / Z_{max}$, Carpenter 1983).

Statistical analysis

Relationships between macrophyte cover or biomass and the various measures of light, trophic status and morphometry were described by regression analysis. These variables were transformed, if necessary to meet statistical requirements of linear regression, following Box and Tidwell (1962) and a stepwise procedure was used to select the best independent variables for each model. The relative contributions of the different regressors in multivariate models were determined by ANOVA (Moesteller and Tukey 1977). The standard error of the estimates were calculated to indicate the error involved in the models. The predictive power of the models was assessed by cross-validation (Draper and Smith 1981). For this purpose 10% of the observations in the data set were randomly selected and the predictions for these obtained from the regression built with the rest of the data set. The procedure was iterated until the number of observations tested equaled approximately 50% of the total data set. The accuracy of the predictions can then be judged by plotting the observed values for the randomly selected data against the values predicted by the regressions built with the remaining observations. The results can be assessed by comparing them to statistics used for evaluating the fit (R^2 and standard error of the estimate).

Data set

The data set included 139 lakes and covered a wide range of values for all variables (Table 1). However, not all variables were measured in all lakes, and therefore the number of observations decreased significantly when multivariate models were attempted. The majority of the lakes were located in Europe (58) or North America (62), but lakes in Africa (6), South Africa (4), Asia (6) and Australia (1) were included. The lakes ranged in latitude from lake Curua-Una, Brazil (Latitude 3^{o} S) to subantartic lakes Sombre, Moss and Changing (Latitude 61^{o} S). The size varied from 2.5 10^6 ha (Lake Chad) to small ponds such as Borax lake, California (0.038 ha), maximum depth ranged from 310 m in Loch Morar, Scotland, to 1 m in some oxbow lakes, Alberta. Secchi depths varied between 0.3 m in extremely turbid lakes like Lake Chilwa, Malawi, to 16 m in clear Lake Leman (France-Switzerland). Low Secchi readings were generally attributable to high algal biomass, however it cannot be taken strictly as an index of trophy because coloured lakes, generally oligotrophic, also have high extinction coefficients, and because low Secchi depths may also be attributable to sediment resuspension as in some large shallow lakes (i.e. Neusiedlersee, Austria). Salinity varied from freshwater to sea water in some coastal lakes, and the data set included 11 lakes with conductivities above 1000 µS cm^{-1}.

Table 1.1 Mean, range and number of observations for the different measures of macrophyte cover and biomass and the environmental parameters correlated to them.

Variable	Mean	Maximum	Minimum	N
A (ha)	7900	2.48 10^6	0.038	141
Zmax (m)	21.8	310.0	1.0	130
Z (m)	7.7	152.0	0.2	116
Sd (m)	2.8	16.0	0.3	102
Ia (kcal cm^{-2} yr^{-1})	109	200	70	139
Lat (degrees)	46.0	69.0	1.0	139
P (mm yr^{-1})	1150	3200	420	139
Lic (days)	93	288	0	139
%Am (percent)	44.1	100.0	0	104
%As (percent)	35.0	100.0	0	82
%Ae (percent)	12.3	100.0	0	77
Rbs (t dry wt. ha^{-1})	3.1	24.6	0.021	51
Rbe (t dry wt. ha^{-1})	15.1	120.0	0.13	28

A = Lake area; Z = Mean depth; Zmax = Maximum depth; Sd = Secchi depth; Ia = Annual surface irradiance; Lat = Latitude; P = Annual precipitation; Lic = Length of ice cover; %Am = Percent lake area covered by macrophytes; %As = Percent lake area covered by submerged plants; %Ae = Percent lake area covered by emergent macrophytes; Rbs = Biomass of submerged plants per unit area colonized; Rbe = Biomass of emergent plants per unit area colonized.

RESULTS AND DISCUSSION

The climatic and morphometric variables that were correlated with macrophyte biomass and cover were not redundant, in that the correlation coefficients among them were not very high (Table 2).

Submerged macrophytes

Both total area covered and total biomass will tend to be greater in larger lakes, but there is no a priori reason to expect that any given standarization (for example division by lake area) will stabilize this effect. Consequently, the effect of lake size must be considered before any other factor can be effectively analyzed.

The analysis showed that the surface area covered by submerged macrophytes (A_s) is not a constant proportion of the lake Area (A) (Fig. 1), but tends to be a smaller proportion in bigger lakes (H_o: exponent = 1, $P<0.05$; Eq. 1, Table 3). The equation for submerged biomass (B_s, Eq. 2, Table 3), indicates that, per unit area, it too is smaller in bigger lakes (H_o: exponent = 1, $P<0.10$; Fig. 2). Thus the relative importance of submerged macrophytes will be, on average, higher in smaller lakes. The reason for the relative reduction of submerged macrophytes in larger lakes is partially related to the positive correlation between lake size and mean depth ($R^2 = 0.41$, $P<0.01$), resulting in larger areas below the depth of maximum penetration of submerged plants.

The analysis indicates that cover is not merely a function of lake area, but that submerged plant cover is relatively greater in lakes with higher underwater irradiance (Eq. 3, Table 3). The underwater irradiance is the single most significant correlate of submerged plant cover. Cross-validation of the model shows that the equation has considerably predictive

Table 1.2 Correlation matrix between the climatic and limnological factors used as regressors of macrophyte abundance. Only values with P<0.05 shown. S =slope; Iz = annual irradiance at the mean depth. Other symbols as in Table 1.

Variables	A*	Z	Zmax	S	Sd	Ia	Lat	P	Lic	Iz
A	-	0.41	0.37	0.70	0.22	0.28	-0.29	0.22	-0.22	0.49
Z		-	0.94	0.20	0.58	-	-	-	-	-
Zmax			-	0.20	0.60	-	-	-	-	-
S				-	0.28	-0.32	0.25	-	-	-0.31
Sd					-	-	-	0.35	-	-
Ia						-	-0.88	0.45	-0.80	0.83
Lat							-	-0.58	0.80	-0.78
P								-	-0.62	0.45
Lic									-	0.80
Iz										-

* Variable log transformed before correlations were calculated

Figure 1.1 The relationship between the surface area covered by submerged (●) and emergent macrophytes (△) and lake area (in ha). Regression lines for submerged (Eq. 1, Table 3) and emergent (Eq. 8, Table 4) macrophytes are shown as continuous and broken lines, respectively.

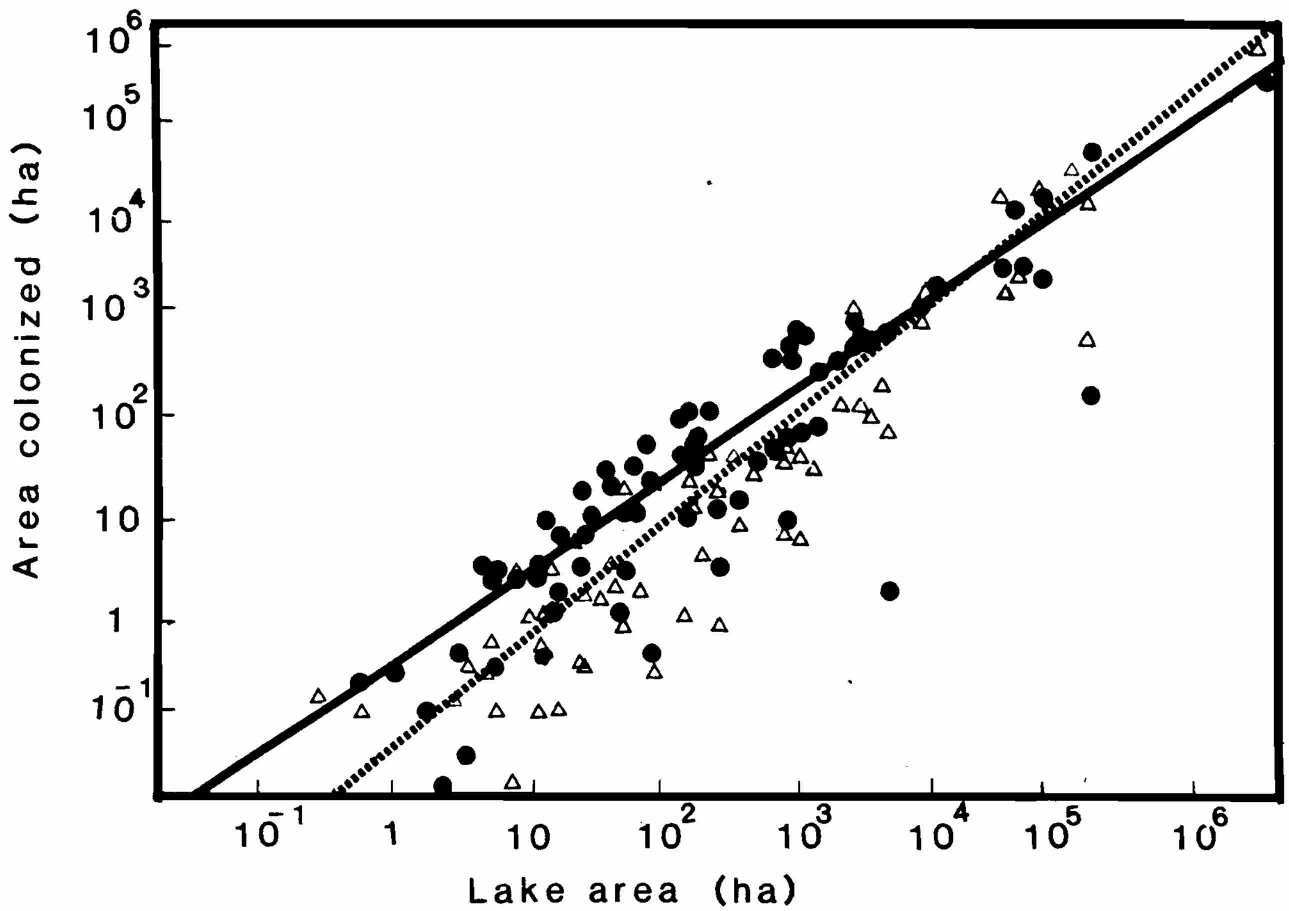


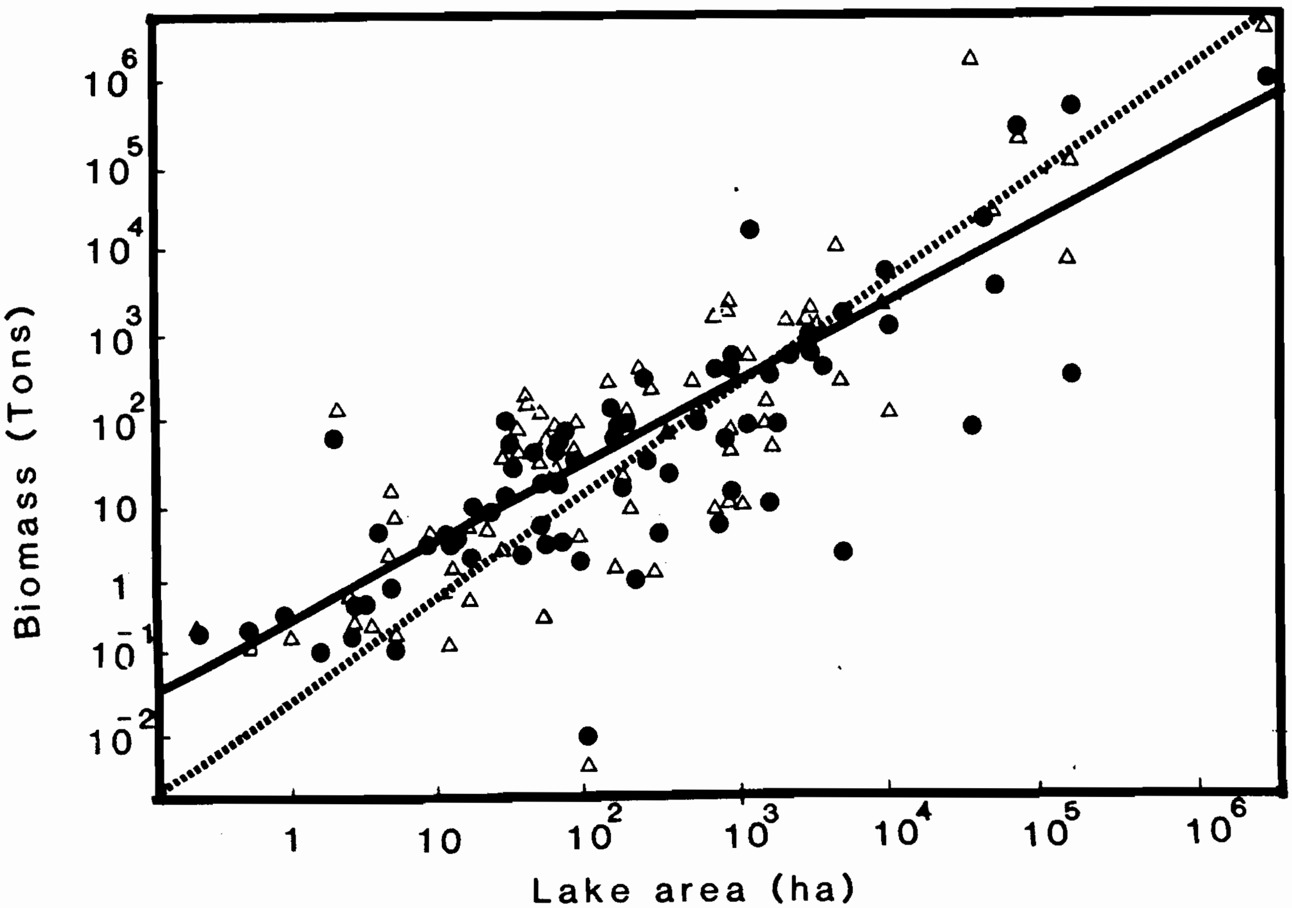
Table 1.3 Regression models describing the total (As) and the percent lake surface (%As) colonized by submerged macrophytes, their total biomass (Bs) and their biomass per unit area colonized (Rbs) as a function of environmental factors. The relationship between biomass and area colonized is also shown. The variable Sal takes values 1 or 0 depending on whether the lake has a conductivity above or below 1000 µS cm^{-1}. Other symbols and units as in Table 1.

	Equation	R^2	N	P	$S.E._{ln\ est}$
(1)	$\ln As = 0.91 \ln A - 1.1$	0.80	76	<0.0001	1.47
(2)	$\ln Bs = 0.89 \ln A - 1.42$	0.59	70	<0.0001	3.04
(3)	$\ln As = 0.94 \ln A + 0.85 \ln I\bar{z} - 3.7$	0.89	51	<0.0001	1.05
(4)	$\ln Bs = 0.95 \ln A + 1.12 \ln I\bar{z} - 4.6$	0.66	56	<0.0001	2.14
(5)	$\ln Bs = 0.99 \ln As + 0.37$	0.84	51	<0.0001	1.26
(6)	$\sqrt{Rbs} = 0.06\sqrt{P} + 0.05\ I\bar{z} - 5.6\ 10^{-4}\ I\bar{z}^2 - 1.3$	0.51	39	<0.0001	0.77*
(7)	$\%As = 1.4\ \bar{I}\bar{z} + 0.07\ Lic - 24\ Sal - 0.90$	0.60	55	<0.0001	11.2**

* $S.E._{est}$ for Rbs is the standard error of the square root of the predicted value.

** $S.E._{est}$ for %As is the standard error of the untransformed percentage.

Figure 1.2 The relationship between lake size and the biomass of submerged (●) and emergent (△) macrophytes (in tons dry wt. ha^{-1}). The regression lines for submerged (Eq. 2, Table 3) and emergent (Eq. 11, Table 4) macrophytes are shown as a continuous and broken line, respectively.

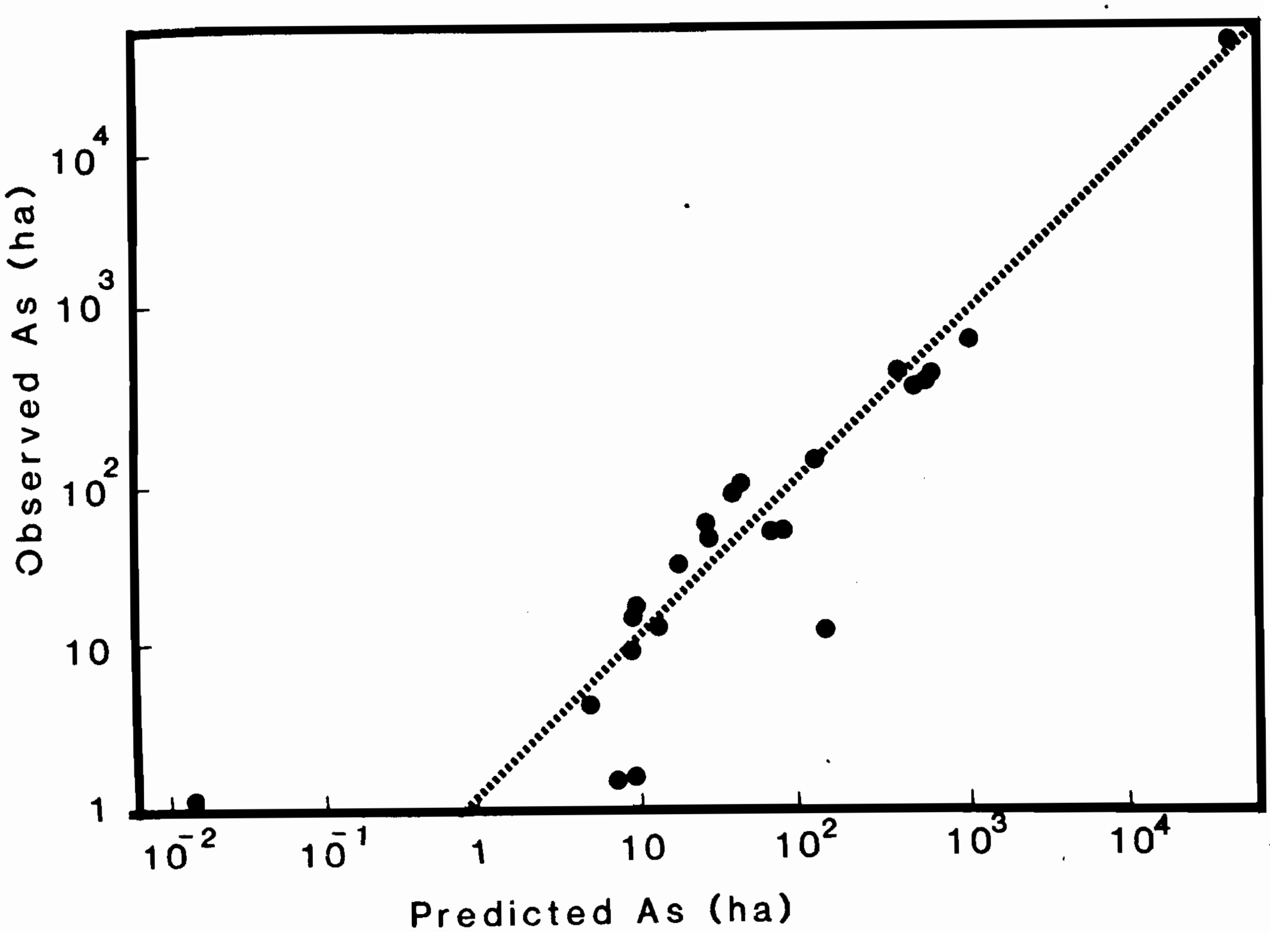


power (R^2 = 0.81, $S.E._{ln\ est}$ = 0.99). The magnitude of the deviations from the calculated values (Fig. 3) show that the uncertainity around the prediction for the area covered is approximately an order of magnitude. Although this is not very precise, the precision is comparable to that of phytoplankton models widely used in lake ecology and management (Dillon and Rigler 1974, Vollenweider and Kerekes 1982) and should, therefore, be of equivalent value. It is, in any case,the only such relationship available.

An analysis of the effect of the various environmental factors on submerged biomass again revealed biomass to increase with increasing underwater irradiance (Eq. 4, Table 3). The relationship between submerged biomass and irradiance was, however, weaker than that for cover and was not improved by the consideration of other factors. While the low resolution of the equation prevents its use for predicting macrophyte biomass, it does show a pattern, providing additional evidence for the important role of light availability on the ecology of submerged macrophytes. However, submerged biomass can be estimated with greater precision (cross validation R^2 = 0.88, ln $S.E._{est}$= 1.49) if the area covered by submerged plants is known (Eq. 5, Table 3).

The importance of underwater light availability in determining the cover and biomass of submerged macrophytes (Eqs. 3 and 4, Table 3) implies that changes in underwater irradiance should lead to parallel changes in submerged cover and biomass at any one site. Such changes can result from changes on 1) climate (that determines the incoming irradiance), 2) the transparency of the water (determining the attenuation of irradiance on the water column) and, 3) the depth of the lake (which determines the extent of the attenuation of irradiance before reaching the bottom). From our approximation of the underwater irradiance ($I_z = I_o\ e^{-z*1.46/Sd}$) it is

Figure 1.3 Cross-validation of the model predicting submerged cover (Eq. 3, Table 3), showing the relationship between the values predicted from the model and observed values for independent sets of data.



evident that changes in incoming irradiance will produce a smaller response of the submerged macrophyte cover than if the water transparency (Sd) or mean depth of the lake (Z) changes. This may well account for the absence of literature evidence for the effect of latitude on cover and biomass of submerged plants and explain, in contrast, why reductions in water transparency have long been associated with a decline in the submerged vegetation (Phillips et al. 1978, Ozimek 1984).

The scatter in the relationship between submerged biomass and the area the plants cover is relatively large (Eq. 5, Table 3) reflecting the great variability in the biomass of submerged plants per unit area colonized. The irradiance received by the submerged plants has been postulated to determine their maximum biomass (Duarte and Kalff 1987). We therefore tested whether differences in underwater irradiance account for the observed variability in submerged biomass per unit area colonized. Regression analysis supported this (Eq. 6, Table 3), indicating that well irradiated lakes support a greater mean submerged biomass per unit area colonized than those with reduced underwater irradiance. However, the relationship is not linear, submerged biomass increasing more slowly at higher light levels, as reflected in the negative Iz^2 term (Eq. 6, Table 3). In addition to irradiance submerged biomass was also positively related to the annual precipitation. This pattern is similar to the positive relationship proposed for phytoplankton (Goldman and Amezaga 1984), and suggests that while the precipitation may represent a small proportion of the total nutrient loading, the fact that it is evenly distributed throughout the lake surface may make it more amenable to enhance plant growth.

The large effect of lake size on cover could overshadow the relationships between cover and environmental factors other than irradiance. These factors might, therefore, be better examined by using the percent lake area covered by submerged macrophytes as the appropiate dependent variable (Eq. 7, Table 3). The results confirm the strong positive relationship between cover (%As) and the mean irradiance within the mean depth of the lake ($\bar{I}\bar{z}$). An analysis of covariance with a dummy variable that discriminates lakes with salinities above and below 1000 µS cm^{-1} further suggests that submerged macrophytes cover a smaller proportion of the area of more saline lakes (Fig. 4), a finding supported by numerous observations. Williams (1978) noted that submerged macrophyte development in lakes is severely affected by salinity, and Hammer (1981) mentions that submerged macrophytes are less abundant in saline lakes. Since some of these observations refer to non-coastal saline lakes, the significant factor appears to be salinity, not vicinity to the sea.

Emergent macrophytes

The relationship between lake size on the one hand and area and biomass of emergent macrophytes on the other also needs to be examined before assesing the effect of environmental factors on cover and biomass. The relationship betweeen the area colonized (Ae) and lake size appears linear (Ho: exponent = 1, P = 0.74; Eq. 8, Table 4). This indicates that emergent macrophytes colonize, on average, 7% of the lake area regardless of the size of the lake and, because submerged plants cover a smaller area in larger lakes, emergent cover will gain importance with increasing lake size (Fig. 1). The constancy of the fraction of lake area covered by emergent plants was also noted for Polish lakes (Planter 1973), where the area covered by emergent plants varied between 9.3 - 12%. In contrast, Spence (1982) postulated that the area colonized by the emergent plants

Figure 1.4 The percent lake area covered by submerged macrophytes as a function of the mean irradiance within the mean depth of the lake. Highly saline lakes (> 1000 µS cm^{-1}) are represented by open circles.

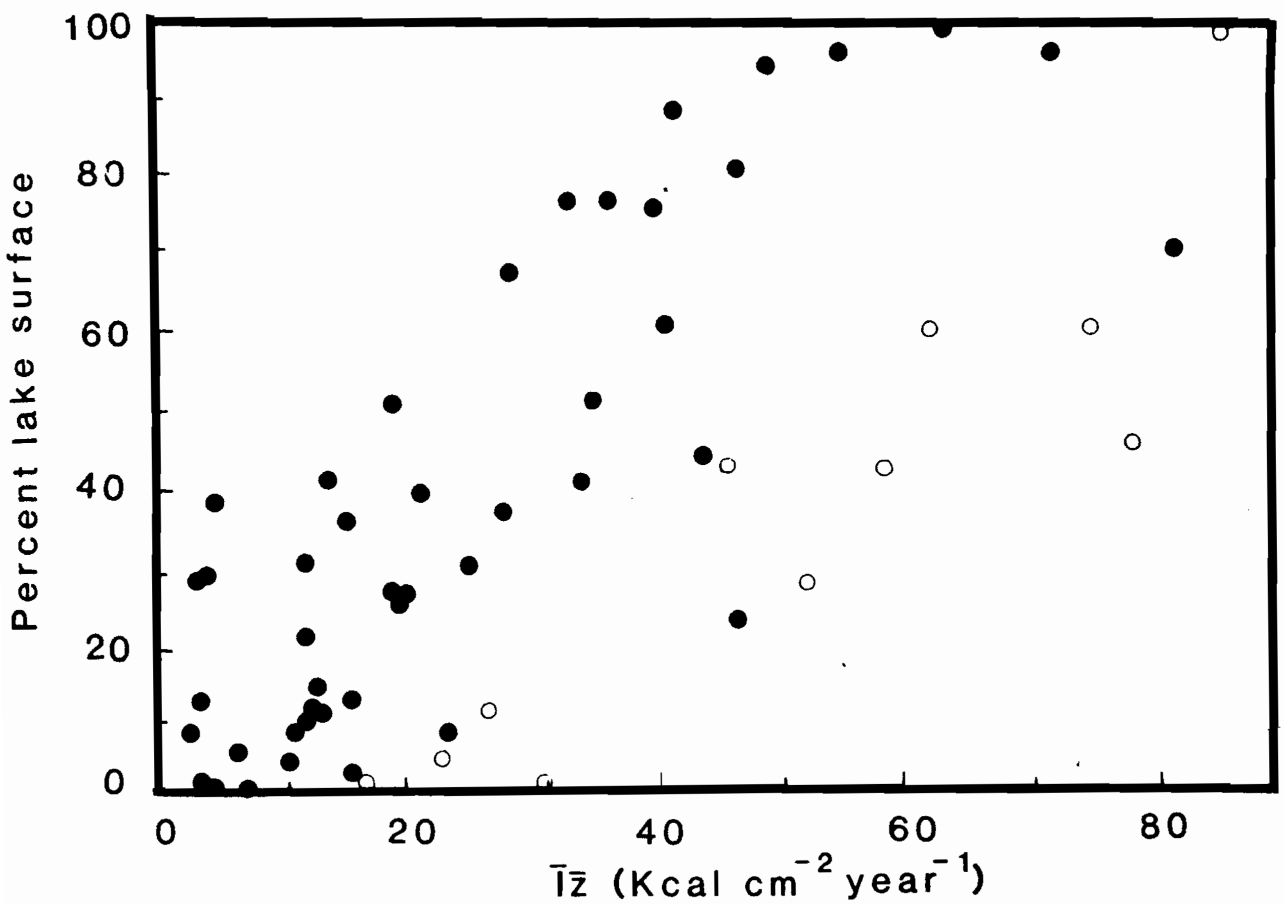


Table 1.4 Models relating the total area (Ae) and percent area (%Ae) colonized by emergent macrophytes and the total biomass (Be) and biomass per unit area (Rbe) colonized by emergent macrophytes to environmental factors. Probability for all regressions < 0.0001. Symbols and units as in Table 1.

Equation	R^2	N	$S.E._{\ln\ est}$
(8) ln (Ae) = 1.0 ln (A) - 2.6	0.87	60	1.33
(9) ln (Ae) = 0.72 ln (A) + 0.69 ln S + 0.72	0.90	60	1.28
(10) %Ae = 2.81 ln (A) - 0.21 Iz - 6.58 ln Zmax	0.41	53	11.59*
(11) ln (Be) = 1.1 ln (A) - 1.4	0.70	36	2.53
(12) ln (Be) = 0.57 ln (A) + ln 1.34 S + 4.77	0.76	32	2.47
(13) ln (Be) = 1.17 ln (Ae) + 0.89	0.91	28	1.45
(14) Rbe = 4.93 ln (A) + 0.75 Lat + 62.5 (Z/Zmax) - 10 ln Z - 6	0.52	26	17.0**

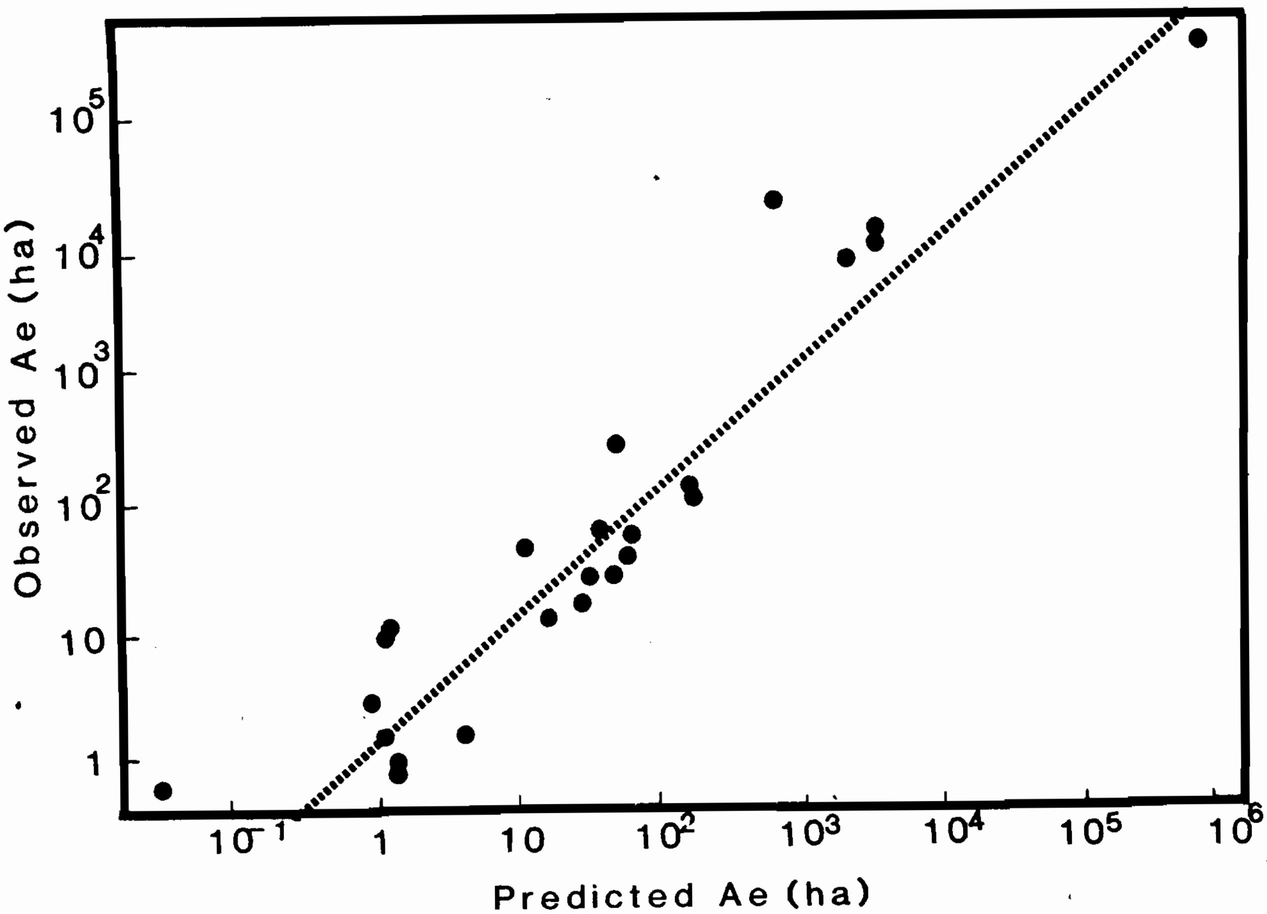
* $S.E._{est}$ of %Ae in percentage.

** $S.E._{est}$ of Rbe in t dry wt. ha^{-1}.

should decline with increasing lake area as a consequence of increased wave action in the littoral. The absence of such a decline here is probably attributable to the increased number of sheltered bays and floodplains in larger lakes, which compensate for the increased wave effect postulated. The relationship between emergent cover and lake area was improved by considering also the steepness of the basin (Eq. 9, Table 4), probably because steep sided lakes have a smaller area suitable for emergent growth. Furthermore, the percent lake area covered by the plants (%Ae) is not constant, but is greater in larger lakes and smaller in deep lakes and lakes receiving high irradiance (Eq. 10, Table 4).

The biomass of emergent plants seems to increase linearly with lake size (Ho: exponent = 1, P = 0.57; Eq. 11, Table 4) and, again as a rough approximation, our analysis indicates that this biomass is about 0.25 t dry wt. ha^{-1} of lake area, the variability in the relationship between emergent biomass and lake size being smaller than that in the analogous one for submerged plants. Biomass of emergent macrophytes also increases more rapidly with lake size than the biomass of submerged ones and is consequently normally greater in larger lakes (Fig. 2). Equation 12 (Table 4) suggests that emergent biomass also declines with increased steepness of the lake basin. The equation relating emergent macrophytes biomass to the surface they cover (Equation 13, Table 4) has a particularly good fit (R^2 = 0.91, Ln $S.E._{est}$=1.4), and can be used to estimate the biomass of emergent macrophytes with better than an order of magnitude resolution (cross-validation R^2= 0.93, Ln $S.E._{est}$= 1.4; Fig 5). When the variation in biomass of emergent plants per unit area colonized was analyzed, we found it to be greater in larger and in shallower lakes and to be positively related to latitude and the depth ratio (Z/Zmax), indicating that pan shaped lakes

Figure 1.5 Agreement between the predicted cover of emergent macrophytes (Eq. 9, Table 4) and independent values of observed cover obtained by cross-validation.



support higher biomass of emergent plants than cone shaped ones, with steeper slopes (Eq. 14, Table 4).

Our models show that the biomass and area colonized by submerged plants are primarily affected by the underwater light regime, as determined by lake morphometry, the extinction coefficient and by latitude. In contrast the total biomass and cover of emergent plants appears unaffected by the available irradiance, but is affected by lake morphometry, since both biomass and cover are related to the steepness and form of the basin and the lake area.

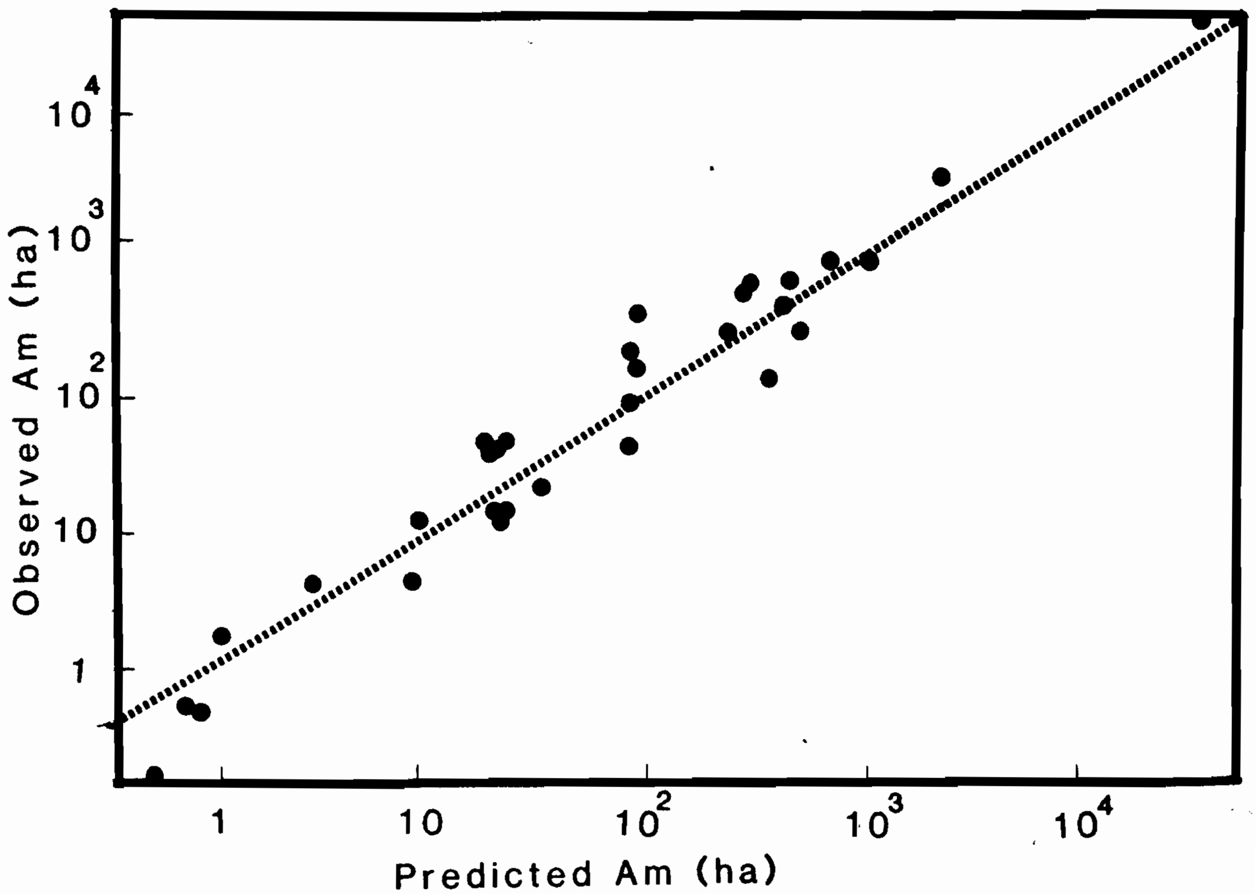
While we considered submerged and emergent macrophytes as separate entities in the analysis, it is clear that they are highly integrated, forming a continuous cover in the littoral zone. Conceivably the surface area covered by emergent and submerged plants together may be more precisely related to environmental variables than emergent or submerged cover separately. This was indeed the case, because the total cover of macrophytes (Am, in ha) is positively related to the annual irradiance at the surface (Ia, kcal cm^{-2} y^{-1}), the annual irradiance at the mean depth of the lake (Iz, kcal cm^{-2} y^{-1}) and the period of ice cover (Lic, days), the equation being:

$$\ln Am = 0.97 \ln Area + 0.98 \ln Iz + 0.009\ Lic + 1.02 \ln Ia \qquad (15)$$

$$R^2 = 0.93,\ N = 71,\ P < 0.0001,\ S.E._{\ln\ est} = 0.86$$

The model is more precise than either the ones describing the emergent or the submerged cover (Cross-validation, $R^2 = 0.94$; $S.E._{\ln\ est} = 0.71$). The scatter around the predicted cover indicates that predictions from this equation are, within half an order of magnitude from the observed values (Fig. 6). This indicates that although submerged and emergent macrophytes affected by different factors in the environment, their separation

Figure 1.6 Cross-validation of the model predicting total macrophyte cover (Eq. 15), showing the values predicted for independent observations.



entails a significant loss of information because they form a continuum in the littoral zone. The relationship obtained suggests that the total macrophyte cover as a whole is largely determined by the underwater light regime and the annual surface irradiance, the later providing a better indication of the light available for growth of emergent plants. The observed relationship between the length of ice cover and the total area covered by macrophytes suggests that, once the effect of reduced irradiance (Iz) has been corrected for, the stable conditions provided by an environment devoided of wave action may enable plants to remain overwinter, without necessarily resulting in increased productivity. In contrast to cover, a consideration of both emergent and submerged macrophytes as a whole did not result in more precise estimates of the total macrophyte biomass, probably because the biomass per unit area is on average one order of magnitude higher on emergents than on submerged macrophytes.

The models describing macrophyte cover are more precise than those for biomass. This may imply a stronger link between surface cover and the factors we studied, but could equally well be the result of the greater patchiness of macrophyte biomass within lakes resulting from the physical heterogeneity of the littoral zone. The latter would result in a large uncertainty around the mean lake values used in our analysis, which may contribute to the greater uncertainty associated with the estimation of the submerged biomass. Nevertheless, the present analysis reveals consistent patterns in macrophyte cover and biomass, and provides the first empirical models for (1) the prediction of the total surface area covered by macrophytes, (2) the area covered by submerged and emergent plants from simple environmental factors, and (3) the prediction of the macrophyte biomass from the more easily estimated area cover.

REFERENCES

Box, G.E.P., and P.H. Tidwell. 1962. Transformation of the independent variables. Technometrics 4: 531-540.

Buscemi, P.A. 1958. Littoral oxygen depletion produced by a cover of Elodea canadensis. Oikos 9: 239-245.

Canfield, D.E.Jr., K.A. Langeland, S.B. Linda, and W.T. Haller. 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. J. Aquat. Plant Manage. 23: 25-28.

________, ________, M.J. Maceina, W.T. Haller, J.V. Shireman, and J.R. Jones. 1983. Trophic state classification of lakes with aquatic macrophytes. Can. J. Fish. Aquat. Sci. 40: 1713-1718.

Carpenter, S.R. 1983a. Submersed macrophyte community structure and internal loading: relations to lake ecosystem productivity and succession, p.p. 105-111. In J. Taggart (ed.), Lake restoration, protection and management. U.S. E.P.A., Washington D.C.

________. 1983b. Lake geometry: implications for production and sediment accretion rates. J. Theor. Biol. 105: 273-286.

Cattaneo, A., and J. Kalff. 1979. Primary production of algae growing on natural and artificial aquatic plants: a study of interactions between epiphytes and their substrate. Limnol. Oceanogr. 24: 1031-1037.

Chambers, P.A., and J. Kalff. Depth distribution and biomass of submersed macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42: 701-709.

Dillon, P.J., and Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767-773.

Draper, N.R., and H. Smith. 1966. Applied regression analysis. Wiley.

Duarte, C.M., and J. Kalff. 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnol. Oceanogr. 31: 1072-1080.

______ , _______ . 1987. Weight-density relationships in submerged macrophytes: The importance of light and plant geometry. Oecologia (Berlin), (In press).

Edwards, R.W. 1968. Plants as oxygenators in rivers. Water Res. 2: 243-248.

Eloranta, P. 1978. Light penetration in different types of lakes in Central Finland. Holarct. Ecol. 1: 362-366.

Goldman, C.R., and E. De Amezaga. 1984. Primary productivity and precipitation at Castle Lake and Lake Tahoe during twenty-four years, 1959-1982. Verh. Int. Ver. Limnol. 22: 591-599.

Goulder, R. 1969. Interactions between the rate of production of freshwater macrophytes and phytoplankton in a pond. Oikos 20: 300-309.

Hakanson, L. 1981. Bottom dynamics in lakes. Hydrobiologia 91: 9-22.

Hammer, V.T. 1981. Primary production in saline lakes. Hydrobiologia 81: 47-57.

Hasler, A.D., and E. Jones. 1949. Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. Ecology 30: 359-364.

Hutchinson, G.E. 1975. A treatise on limnology. Vol. III. Limnological botany. Wiley.

Kouzoun, V.I., A.A. Solokov, M.I. Budyko, K.P. Voskresensky, G.P. Kalinin, A.A. Konoplyanstser, E.S. Korotkevich, amd M.I. Lvovich (eds.). 1977. Atlas of world water balance. Hydrometeorological Publishing House, UNESCO.

Landsberg, H.E., H. Lippmann, K.H. Pafen, and C. Troll. 1966. World maps of climatology. Springer-Verlag.

Magnin, A. 1893. Reserches sur la vegetation des lacs du Jura. Rev. Gen. Bot. 5: 241-257, 303-316.

Margalef, R. 1984. Limnologia. Omega.

Maristo, L. 1941. Die seetypen Finnlando auf floristracher und vegetations-physiognomischer. Grundlage. Ann. Soc. Zool. Bot. Vanamo 15(5).

Moesteller, F., and J.W. Tukey. 1977. Data analysis and regression. A second course in statistics. Addison-Wesley Publishing Co.

Ozimek, T., and A. Kolwalczewski. 1984. Long-term changes of the submerged macrophytes in eutrophic Lake Mikolajskie (North Poland). Aquat. Bot. 9: 1-11.

Pearsall, W.H. 1917. The aquatic and marsh vegetation of Esthwaite water. J. Ecol. 5: 180-201.

_______ . 1920. The aquatic vegetation of the English lakes. J. Ecol. 8: 163-201.

Phillips, S.L., D. Eminson, and B. Moss. 1978. A mechanism to account for macrophyte decline on progressively eutrophicated freshwaters. Aquat. Bot. 4: 103-126.

Planter, M. 1973. Physical and chemical conditions in the helophyte zone of the lake littoral. Pol. Arch. Hydrobiol. 20: 1-7.

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

Riley, G.A. 1957. Phytoplankton of the North Central Sargasso Sea. 1950-1952. Limnol. Oceanogr. 2: 252-270.

Shuter, B.J., D.A. Schlesinger, and A.P. Zimmerman. 1983. Empirical prediction of annual surface cycles in North American lakes. Can. J. Fish. Aquat. Sci. 40: 1838-1845.

Smithsonian Institute. 1939. Smithsonian meteorological tables. Smithsonian Institute, Washington, D.C.

Sozska, G.J. 1975. Ecological relations between invertebrates and submersed macrophytes in the lake littoral. Ekol. Pol. 23: 393-415.

Spence, D.H.N. 1967. Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. J. Ecol. 8: 163-204.

_______ . 1975. Light and plant response in freshwater. p.p. 93-133. In G.C. Evans, R. Bainbridge, and O. Rackman (eds.). Light as an ecological factor. II. Blackwell.

_______ . 1982. The zonation of plants in freshwater lakes. Adv. Ecol. Res. 12: 37-125.

Straskraba, M. 1980. The effect of physical variables on freshwater production: analysis based on models, p. 13-84. In E.D. Le Cren and R.H. Lowe-McConnell (eds.). The functioning of freshwater ecosystems. Cambridge Univ.

Walker, T.A. 1982. Use of a Secchi disc to measure attenuation of underwater light for photosynthesis. J. Appl. Ecol. 19: 539-544.

Westlake, D.F. 1965. Theoretical aspects of the comparability of productivity data. Mem. Ist. Ital. Idrobiol. 18 (Suppl.): 313-322.

_______ . 1974. Sampling techniques and methods for estimating quantity and quality of biomass (macrophytes), p.p. 32-41. In R.A. Vollenweider (ed.). A manual of methods for measuring primary production in aquatic environments. I.B.P. Handb. No. 12. Blackwell.

Whitfield, A.K. 1984. The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a Southern African coastal lake. Estuarine Coastal Shelf Sci. 18:

315-329.

Wiley, J.L., R.W. Gorden, S.W. Waite, and T. Powless. 1984. The relationship between aquatic macrophytes and fish production in Illinois ponds: a simple model. N. Am. J. Fish. Manage. 4: 111-119.

Williams, W.D. 1978. Inland waters. p.p. 19-40. In H.A. Nix and M.A. Elliot (eds.), Managing aquatic ecosystems. Proc. Ecol. Soc. Aust. Vol.8.

Chapter II

Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities

ABSTRACT

The hypothesis that the morphometric characteristics of the littoral zone of lakes are a major determinant of submerged macrophyte biomass was tested in Lake Memphremagog (Québec-Vermont) by studying the relationship between maximum biomass of submerged macrophytes and physical and chemical characteristics of the littoral zone. The slope of the littoral zone accounted for 72% of the observed variability in maximum submerged macrophyte biomass (MSMB). By also incorporating sediment organic matter the variance explained was raised to 76%. A model based on only slope as predictor of MSMB was improved by considering slopes higher and lower than 5.3%:

slope > 5.3% MSMB (g. fresh wt m^{-2}) = $-29.8 + 1403\ slope^{-0.81}$;

slope < 5.3% MSMB (g. fresh wt. m^{2}) = $13.2. + 3434\ slope^{-0.81}$.

The power of these two equations to predict the MSMB in a variety of temperate lakes was high ($r = 0.87$, $P<0.0001$). However, the temperate zone model overestimates the MSMB in highly turbid lakes where irradiance rather than slope is pre-eminent and underestimates the biomass in semitropical and tropical lakes.

INTRODUCTION

Submerged aquatic macrophytes play a major role in the dynamics of shallow lakes and the littoral zone of many large lakes . Their abundance influences the trophic status (Carpenter 1983) and phytoplankton biomass levels (Landers 1982) of shallow lakes. Their surfaces provide a substrate for readily grazeable epiphytes (Cattaneo and Kalff 1980) and their abundance affects fish populations (Wiley et al. 1984). When their growth is excessive, it affects the economic potential of lakes (Holm et al. 1969). Consequently, there is growing interest in the identification of the factors that control macrophyte development and the extent of their impact on lake ecosystems (e.g. Adams and Prentki 1982).

Since the successful development of nutrient-based models for predicting phytoplankton biomass (Vollenweider 1968; Dillon and Rigler 1974), studies have focused on nutrients as the principal determinants of macrophyte growth and biomass. However, the results have been inconclusive, some studies reporting nutrient limitation of submerged macrophyte biomass (e.g. Schlott et al. 1984; Lind and Cottam 1969) and a positive effect of nutrients on biomass (Ozimek 1978) and others reporting that macrophyte populations are unlikely to be limited by nutrient levels (Carpenter and Adams 1977). In contrast to the clear coupling of nutrient levels and phytoplankton biomass, the link between nutrient levels and submersed macrophytes is unclear (Devol and Wissmar 1978) and macrophyte control remains an elusive goal. While other research has shown the effect of light (e.g. Jupp and Spence 1977a; Barko et al. 1982) and wave action (Jupp and Spence 1977b) on macrophyte biomass, this information appears insufficient to explain the broad differences in submersed macrophyte biomass often observed within lakes.

It may be that the relative weakness of such relationships for macrophytes derives from the physical heterogeneity of the littoral area. Topographic and morphometric differences result in differences in littoral dynamics caused by associated variations in slope, wave action, and the input of allochtonous materials. Littoral slope in particular can be a major factor controlling the physical characteristics of the sediment because it affects sediment stability and the deposition of fine nutrient-rich materials (Hakanson 1977). Variation in slope can also modulate wave action in the littoral. The influence of littoral slope on aquatic macrophyte biomass has been suggested by several investigators (e.g. Pearsall 1917; Margalef 1984), who noted that submerged macrophyte biomass decreases where the slope nearshore is steep. However, no quantitative relationship describing this trend has yet been produced.

We will first examine and quantify the relationship between littoral slope and macrophyte biomass in a single lake to determine the strength of the relationship suggested relative to the influence of other factors that contribute to habitat heterogeneity, such as exposure to waves and sediment type. We will then test the hypothesis that lake morphometry is the prime determinant of the maximum submerged macrophyte biomass (MSMB) and show that a model developed in Lake Memphremagog, with its highly variable contours and exposures, is a good predictor of the biomass elsewhere in the temperate zone.

MATERIALS AND METHODS

The study was carried out in dimictic and oligo- to mesotrophic Lake Memphremagog (Québec-Vermont), which differs greatly in littoral morphometry and wave exposure along its 45-km length (see Pace 1984).

We chose sites by dividing a map of the littoral zone into 500 uniformily spaced sections, using topographic and bathymetric information to infer slope and fetch for all the sections. Ward's clustering criterion (SAS inst. 1982) was then applied to group the sites into 44 clusters covering the widest combination of slope and fetch. For each cluster the site with the smallest Euclidian distance (Orloci 1975) to the centroid of the cluster was selected for macrophyte and sediment sampling.

The "weighted effective fetch" was calculated by a modification of the Beach Erosion Board (1972) method. The distance from each sampling station to the farthest point visible on the shore was determined for the eight compass bearings (N, NW, W, SW, S, SE, E, NE) and for angles of plus or minus 11.25 and 22.5 degrees of each bearing. The distances measured for a given bearing were combined according to the formula:

$$F= \sum D_i * \cos_i/5$$

where F is the effective fetch (km), and D_i is the distance for i degrees of the bearing (i= $\pm$0, $\pm$11.25, $\pm$22.5). The effective fetch for each of the eight compass bearings and the wind frequencies from the same bearing obtained from records of the past 3 years by a metereological station at the north end of the lake were combined to yield a single value of fetch with the formula:

$$WEF = \sum F_i wf_i$$

where WEF is weighted effective fetch, F_i is fetch for bearing i, and wf_i is wind frequency for bearing i. These calculations provide corrections for wave modifications due to lake morphometry and also take into account the particular wind regime of the area studied, and thus provide reliable estimations of wave exposure at particular sites along the lake.

We got a more accurate estimate of the littoral slope for each site by measuring the angle between water and sediment surfaces along a transect perpendicular to the shore, using an echosounder (Si-Tex Honda). Littoral slope estimates for these sites calculated from the 10-m-depth isopleth of a bathymetric map (1:31,650) were used to compare data from other lakes for which slopes were also taken from bathymetric maps.

Early in August the depth of maximum submerged macrophyte biomass (MSMB) was estimated for each site in Lake Memphremagog by sampling the biomass along two transects perpendicular to the shore and sampled at this depth 3-5 times between mid-August and mid-September, the period of maximum submerged macrophyte biomass. All plants within a quadrat (0.78 m^2) were harvested by Scuba divers and kept refrigerated until processed. Plant material was washed free of animals and detritus and the fresh weight determined after removing excess water by spinning the plants for 3 min in a salad spin-dryer.

We measured sediment characteristics from two cores (4-cm i.d.) taken within the quadrats on each sampling date and kept refrigerated until processed (within 24 h). The upper 5-cm stratum was extruded, and, for each core, sediment water content was calculated from the decrease in weight after drying overnight at 110 C. Organic matter was determined from mass loss after oxidizing the sediments overnight at 550 C. Total phosphorus was measured according to Andersen (1976). We measured the Secchi disk depth early in September at 30 of the 44 stations as an index of the possible limitation of macrophyte biomass by light.

To allow comparison of our data with those from the literature, we determined the littoral slopes of the data obtained from the literature from bathymetric maps, using the slope between the shoreline and the 5- or 10-m depth contour, where the MSMB was measured at the time of maximum biomass (August to mid-September for temperate lakes). All literature data were transformed to grams fresh weight per square meter by assuming dry weight to be 10% of fresh weight, and dry weight to have an ash content of 20% and an organic carbon content of 37% (Westlake 1963).

Linear regression was used to model the relationships between variables unless we found an increase precision or a significant improvement in the distribution of residuals by using non-linear models. A stepwise linear regresssion procedure was used to select the independent variables for each model. Independent variables were, when necessary, transformed (Box and Tidwell 1962) to meet statistical requirements of linear regression. When the relationship between the dependent and independent variables changed for different ranges of the independent variable, the data set was split for additional analysis at the midpoint between those two adjacent values of the independent variable where the following expresion was maximal (see Breiman et al. 1984):

$$RSS = DSS - (D1SS + D2SS)$$

where RSS is the remaining sum of squares about the mean, DSS the sum of squares about the mean for the entire data set, and D1SS and D2SS the sum of squares about the means of the resulting groups. Linear regressions were then determined between the dependent and the independent variables for each group and the slopes of the two regressions compared with a t-test. When the slopes for the two groups were significantly different ($P < 0.01$), the separate equations were used to model the relationship between the variables.

RESULTS

The range covered by the variables studied is given in Table 1. The slope of the littoral was best correlated with MSMB (Table 2). Other variables significantly correlated with MSMB were fetch and sediment organic matter. The relationship between slope of the littoral and MSMB was further explored by regression analysis. A power transformation of -0.81 was found to be the best transformation to linearize the relationship between MSMB and slope of the littoral. The model obtained explained 72% of the variance (Fig. 1). The equation predicting MSMB from slope was:

$$MSMB = 122 + 986\ slope^{-0.81} \qquad (1)$$

$$R^2=0.72;\ N=44;\ F=110;\ P<0.0001$$

$$S.E._{int}= 62,\ S.E._{slope}= 94$$

The relationship between MSMB and slope has an uneven distribution of residuals, with most higher slopes having negative residuals. This suggested that the relationship between littoral slope and macrophyte biomass may differ for gentle and steep slopes. Further analysis confirmed that a littoral slope of 2.2% provided the best division of the data set, reducing the variance in MSMB by 47% upon dividing the data between sites with slope higher or lower than 2.2%. When the two data sets were analyzed separately, the slopes of the two resulting regression equations indeed differed significantly (P<0.01), indicating a different relationship between MSMB and littoral slope for high and low slopes. The equations obtained for the two categories were

slope < 2.2%

$$MSMB = 103.7 + 885\ slope^{-0.81} \qquad (2)$$

$$R^2=0.67;\ N = 13;\ F = 80;\ P<0.001$$

Table 2.1 Range and means for the variables measured at 44 stations in lake Memphremagog during August 1984.

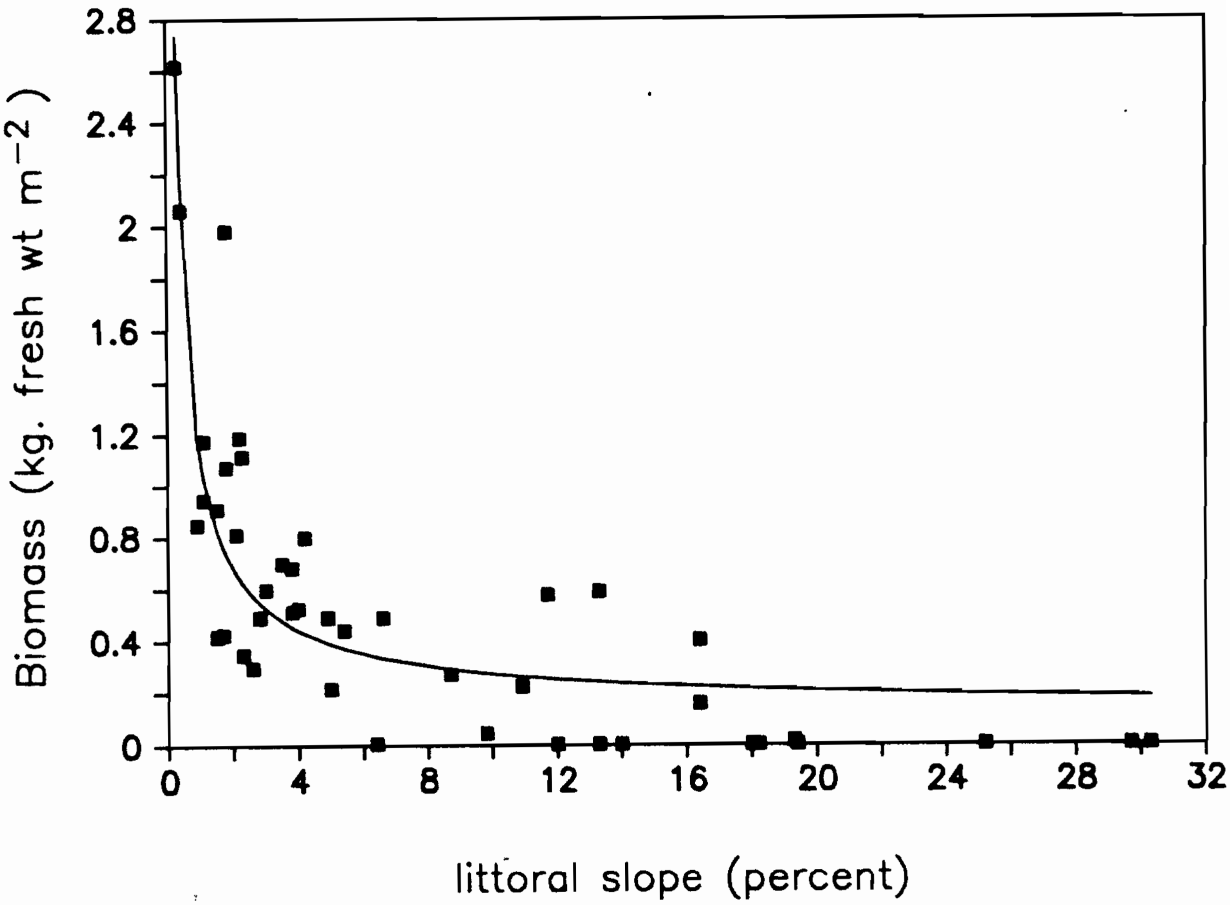
Variable	Minimum	Maximum	Mean
Sed. Water content (%)	18.6	97.0	47.1
MSMB (g. fresh wt. m^{-2})	0.0	2614.4	553.8
Littoral slope (%)	0.3	30.3	8.3
Fetch (Km)	0.18	9.9	3.4
Org. matter (%)	1.0	45.4	7.5
Total P (mg g^{-1})	0.04	2.1	0.6

Table 2.2 Correlation coefficients between the measured variables in Lake Memphremagog (n=44, Total P n = 32). Units given in Table 1.

Variable	Water content	MSMB	Slope	Fetch	Org. matter	Total P
Water content	-	0.37*	-0.12	-0.35*	0.81**	0.28
MSMB		-	-0.62**	-0.36*	0.22	-0.01
Slope			-	0.05	0.06	0.05
Fetch				-	-0.31*	-0.14
Org. matter					-	0.17
Total P						-

* Significant (P<0.05); ** Highly significant (P<0.005).

Figure 2.1 Maximum submerged macrophyte biomass (g. fresh wt. m^{-2}) versus the slope of the littoral zone for the Lake Memphremagog stations. The line represents the regression equation (Eq. 1).



Slope >2.2%

$$MSMB = -26.34 + 1517\ slope^{-0.81} \quad (3)$$

R^2=0.47; N = 31; F = 80.9; P<0.001

The variance in MSMB explained by littoral slope is greater at gently sloped sites (<2.2%) than at steep sites. Furthermore the relationship between the different variables measured differs for the two slope categories (Table 3), with fetch having a significant correlation with MSMB only at gentle slopes and sediment characteristics being highly correlated with each other in steep sites.

The proportion of the variance of MSMB explained was significantly (P<0.01) increased by considering not only slope (Eq. 1) but also the percent sediment organic matter. A model predicting MSMB with both predictors was:

$$MSMB = 34 + 12.3\ Org.\ matter + 979\ slope^{-0.81} \quad (4)$$

R^2= 0.76; n=44; F=67; P<0.0001

$S.E._{int}$= 25.7, $S.E._{Org.\ matter}$=3.9, SE_{slope}= 80.8

Other independent variables did not significantly improved the relationship to maximum submerged macrophyte biomass.

When, for comparison with the literature, we determined slopes from a bathymetric map, the critical value separating the relationship for steep and gentle slopes was 5.3%. The equations predicting MSMB from these slopes were

Slope > 5.3% (5)

$$MSMB = -29.8 + 1403\ slope^{-0.81}$$

R^2=0.60, n=28, F=40.08 (P<0.001)

$S.E._{int}$=18.4, $S.E._{slope}$= 221

Table 2.3 Differences in correlation between the variables measured in Lake Memphremagog sites with slope >2.2% and <2.2%. Symbols and units given in Table 1. NS = Not significant (P>0.05).

Variable		MSMB Fresh	MSMB Dry	Sed. water content	Org. matter
Sed. water content					
	>2.2%	NS	**	-	***
	<2.2%	*	NS	-	**
Slope					
	>2.2%	**	**	NS	NS
	<2.2%	*	*	NS	NS
Fetch					
	>2.2%	NS	NS	NS	NS
	<2.2%	**	*	NS	NS
Total P					
	>2.2%	NS	NS	***	***
	<2.2%	NS	NS	NS	NS
Org. matter					
	>2.2%	NS	*	***	-
	<2.2%	NS	NS	**	-

* P < 0.05; ** P<0.01; *** P<0.005

Slope < 5.3% (6)

$$MSMB = 13.2 + 3434\ slope^{-0.81}$$

$$R^2=0.79,\ n=16,\ F=37.66\ (P<.001)$$

$$S.E._{int}= 11.4,\ S.E._{slope}= 354$$

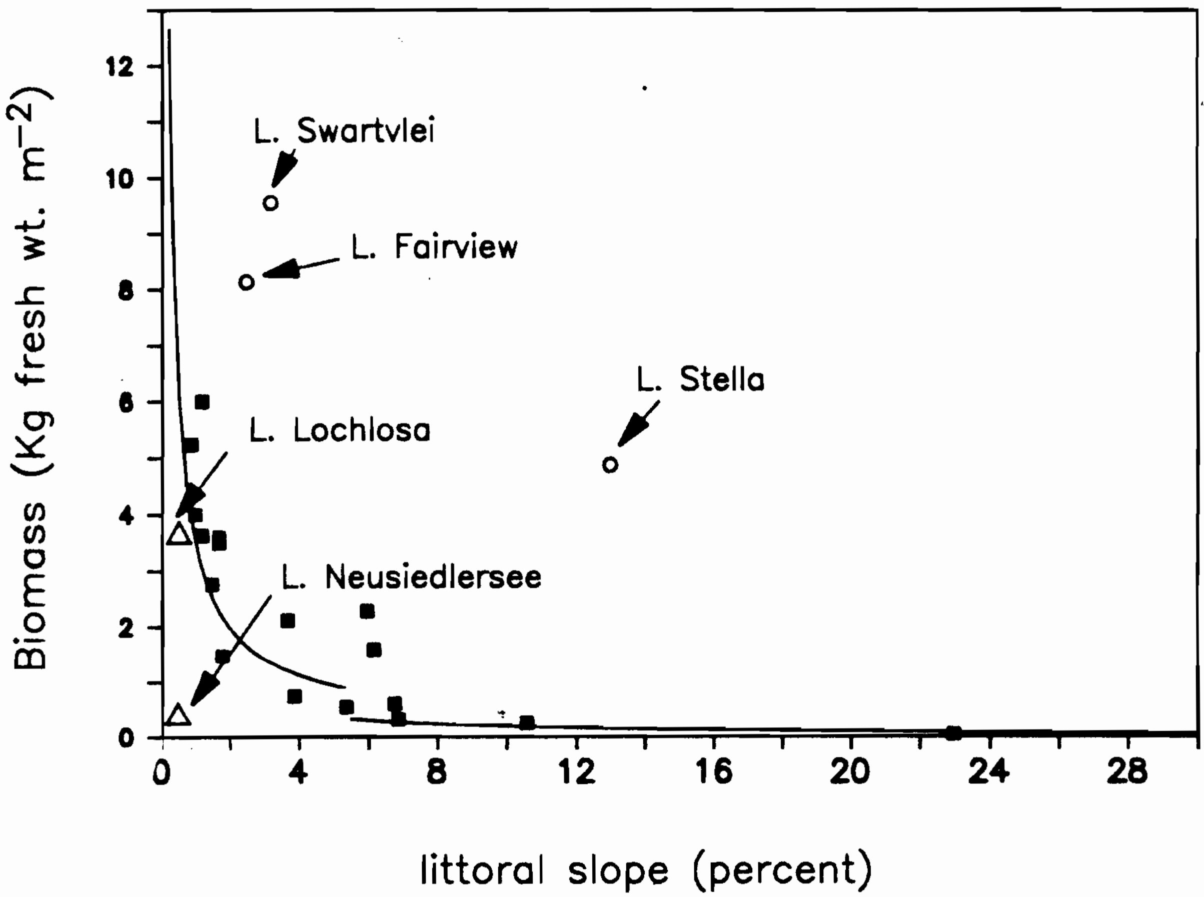
To test the power of these relationships for other lakes, we compared values form the literature with predictions made from equations 5 and 6 (Fig. 2, Table 4). The high coefficient of determination (R^2=0.76) shows that our models are able to make reasonably good predictions of MSMB in temperate lakes with mean Secchi disk depths > 2 m. The slope of the linéar regession between the observed and predicted values does not differ from 1 and the intercept is not different from 0 [slope 1.105, Ho: slope = 1 (P = 0.49); intercept = 48.7, Ho: intercept = 0 (P = 0.39)], so predictions are not obviously biased. However, the model underestimates the observed biomass slightly (sign test, P < 0.05) by, on average 15%.

Table 2.4 Observed submerged maximum biomass (g fresh wt m^{-2}), its associated slope (%), dominant species in the community, sampling method used, and the biomass predicted for temperate lakes by the Lake Memphremagog model (Eqs. 5 and 6).

Lake	Location	Obs. MSMB	Slope	Pred. MSMB	Dominant species	Sampling	Reference
Magog	Quebec	2115	3.7	1189	Mixed comm.	SCUBA	Chambers and Kalff 1985
Lovering	"	738	3.9	1152	Mixed comm.	SCUBA	Chambers and Kalff 1985
Massawippi	"	3627	1.2	2882	M. spicatum	SCUBA	Chambers and Kalff 1985
Bowker	"	250	10.6	177	E. canadensis	SCUBA	Chambers and Kalff 1985
Brompton	"	314	6.9	262	P. praelongus P. robinsii	SCUBA	Chambers and Kalff 1985
Orford	"	41	23.0	80	P. crispus I. lacustris	SCUBA	Chambers and Kalff 1985
Waterloo	"	2759	1.5	2363	E. canadensis	SCUBA	Chambers and Kalff 1985
G. Langso	Denmark	2280	6.0	319	L. uniflora	SCUBA	Nygaard 1958
Wabee	Indiana	1595	6.2	287	P. illinoensis	Dredge	Wohlschlag 1950
Mendota	Wisconsin	1482	1.8	2099	M. exalbescens	SCUBA	Lind and Cottam 1969
Mikolajskie	Polland	540	5.4	328	P. perfoliatus	SCUBA	Ozimek 1978
Cox Hollow	Wisconsin	3500	1.7	2185	C. demersum	Dredge	Richardson 1974
T. Valley	Wisconsin	6000	1.2	3563	C. demersum	Dredge	Richardson 1974
Wingra	Wisconsin	4000	1.0*	3447	M. spicatum	SCUBA	Nichols 1971
Llyn Gwynant	England	600	6.8	267	L. uniflora	SCUBA	Wode and Beresford 1979
D'Endine	Italy	3603	1.7	2226	C. demersum	SCUBA	Guilizzoni and Saraceni 1974
Opinicon	Ontario	5240	0.9	3857	M. spicatum	SCUBA	Keast 1984

* Slope from Baumann et al. (1973)

Figure 2.2 Comparison of the maximum submerged biomass (kg fresh wt m^{-2}) for lakes in the literature with the biomass predicted from their littoral slopes. The different lake types are temperate lakes for which the model was designed (■), subtropical lakes (o), and highly turbid lakes (Δ). The lines represents values predicted from Eqs. 5 and 6.



DISCUSSION

Although the possible influence of slope on submerged macrophyte biomass was suggested by Pearsall (1917) and subsequently reiterated (e.g. Margalef 1984), this is the the first study to quantify the relationship and use it predictively. Our results show the strong relationship between the slope of the littoral and the biomass of submerged macrophyte communities. The reason for this strong correlation cannot be inferred from the results presented, but the data suggests some explanations as more probable than others. The first and most obvious difference between steep and gently sloped littorals is the difference in physical stability of the sediments. A gently sloped littoral allows the deposition of fine materials, while steep slopes are mainly areas of erosion and sediment transport (Hakanson 1977). The observed differences in the correlation coefficients between macrophyte biomass, fetch, and sediment characteristics for sites with slopes above and below 2.2% further suggests that the differences are the result of a mechanism linked to slope. The absence of a correlation between fetch and MSMB at high slopes (Table 3) indicates that waves are unlikely to be the factor responsible for the decreased MSMB in steep sites. Instead the existance of a slope break point (2.2 - 5.3%), below which the relationship between sediment characteristics and MSMB changes, strongly points to slope and the associated differences in water content of the sediment (Selby 1982) as factors that allow sediment slumping or debris flow on steep slopes but not on shallow ones. Hakanson (1977, p. 406) was the first to note a threshold value when he reported that "the physical character of the surficial sediments is, as given by the water content, practically independent of the slope for inclinations less than 3.8%". His critical value is very close to our threshold value between MSMB and slope (2.24 %). Threshold values related to slopes are an indication of slumping, with slumping by gravity alone having been reported for underwater slopes as low as 0.5% (Prior and Suhayda 1979).

There have been many, largely unsuccessful, attempts to link macrophyte biomass to sediment and underwater light conditions (e.g. Barko et al. 1982; Barko and Smart 1983; Chambers and Kalff 1985). It is now apparent that the principal reason for the lack of success was no that biomass is unrelated to sediment variables, but rather that biomass is strongly related to slope, whereas sediment variables bear no constant relationship to slope (Table 3). We believe that the higher threshold value (5.3%) obtained when we used maps, rather than echosounder transects at the sampling sites results form the lack of precision and a scale-dependent bias in estimating slopes from bathymetric maps. This difference in the precision of the maps used probably is responsible for the tendency of the Memphremagog models to underestimate the MSMB in other lakes, since the Memphremagog bathymetric data had the largest scale of those included.

Sediment organic matter has been shown to influence macrophyte growth, at least under laboratory conditions, but whether the influence is positive or negative appears to depend on both the nature and concentration of the organic matter (Barko and Smart 1983). We found an increase in MSMB with increasing sediment organic matter over the range encountered in L. Memphremagog (Table 1), but whether this correlation reflects a direct effect of organic matter content, an indirect effect of the energy climate in the littoral, or is simply the consequence of heavier macrophyte growth remains to be solved.

The good correlation between the predicted biomass and observed MSMB values from the literature (Table 4, Fig.2), makes it evident that the two Lake Memphremagog equations (Eq. 5,6) can be used to predict the biomass of submerged macrophytes over a wide range of conditions (Table 4). The models also correctly predict the direction of change in a shallow lake in which the mean depth, and consequently the slope, was increased as the result of dredging. When the mean depth of Lilly lake, Wisconsin, was increased from 1.4 to 2.3 meters, the mean biomass decreased from 421 to 235 g dry wt. m^{-2} between 2.5 and 4 m (Nichols 1984) as would be predicted from the change in slope associated with the increased mean depth. Unfortunately, Nichols (1984) did not give sufficient information to apply our model directly to the data of Lilly lake. Slope also has an effect on plant abundance above the waterline (Sain et al. 1984), suggesting that the relationship observed between slope and submerged plant biomass extends to different plant communities as well.

That models developed in one lake are useful in making a first prediction of MSMB in a wide variety of lakes is an affirmation of the great importance of slope and associated sediment conditions on macrophyte biomass. That our model, on average, underestimates the literature biomass by 15% is a minor flaw, probably attributable to the exceptionally wide contour intervals (10 m) available for Lake Memphremagog. These wide intervals overlook the normally gently sloped shelf present before the slope steepens toward the sublittoral; as a consequence wide intervals overestimate the average slope and underestimate the biomass. This is evident from the fact that the contour maps overestimated the littoral slope, as measured with an echosounder, at 80% of the sites. This error is probably responsible for the modest 15% underestimate of temperate zone biomass with the Lake Memphremagog model.

Our model was developed and tested for temperate lakes ranging from oligotrophic to eutrophic and is, therefore, not expected to be appropiate for either hypereutrophic lakes with Secchi disk readings of less than < 2 m or tropical lakes. Thus, highly turbid Neusiedlersee (Austria: Schiemer and Prosser 1976) and Lochlosa (Florida, Canfield et al. unpubl. data) with Secchi disk readings of 0.5 and 0.7 meters had biomasses a 47- and 3.6-fold lower than predicted, supporting the observation (Ozimek and Kowalczewski 1984) that highly turbid lakes support little biomass because of light limitation. In contrast, tropical and subtropical lakes Swartvlei (South Africa, Howard-Williams and Allanson 1981), Fairview, and Stella (Florida, Canfield et al. unpubl. data) have a MSMB 4- to 6 fold greater than predicted, probably linked to the much greater solar radiation received during the long growing season (CHAPTER 1). The relatively small reduction of biomass in highly turbid subtropical L. Lochlosa compared to turbid but temperate Neusiedlersee may well reflect the general tendency for subtropical lakes to support a higher biomass.

The correlation between observed and predicted biomass in temperate lakes (Fig. 2) is certainly lowered as the result of the widely varying sampling techniques used in the literature. For example, our model underestimates the MSMB where dredges rather than SCUBA divers were used to collect the plants (Table 4). The error was significantly higher for the former (t-test, $P<0.05$), suggesting a possible overestimate of biomass obtained with dredges. Forsberg (1959) too reported that samplers consistently overestimate the biomass of submerged macrophytes when compared with hand-cutting techniques. Richardson (1974), who used a surface operated device to estimate macrophyte biomass, acknowledges that he probably overestimated the biomass because Elodea canadensis formed a thick mat that could hardly be discriminated from the biomass enclosed in the sampling area.

The influence of nutrient concentrations on MSMB appears to be small compared to their role in determining phytoplankton biomass. This is further evident from the modest responses of macrophytes to in situ fertilization in Lake Memphremagog (Anderson 1985), pointing to the stronger relationship between morphometry and biomass of submerged macrophytes.

We have demonstrated and quantified the importance of littoral slope to the maximum biomass of submerged macrophytes in a wide variety of lakes, that differed greatly in their macrophyte species composition (Table 4). The models produced are not applicable to highly turbid temperate lakes and subtropical and tropical lakes; the influence of large differences in light levels is shown by the poor estimations of MSMB based on slope of the littoral alone in such lakes. Further research on the interaction of slope and light levels on MSMB is needed if more universal models are desired. Following a period in which much attention has been focussed on nutrient supply rates to lakes, the demonstration of the relevance of lake morphometry to macrophyte as well as to phytoplankton biomass (Sakamoto 1966) and fish catches is an appropiate reminder that lake morphometry should not be overlooked in the characterization of lake productivity.

REFERENCES

Adams, M.S., and R.T. Prentki. 1982. Biology, metabolism and functions of littoral submersed weedbeds of lake Wingra, Wisconsin, USA: A summary and review. Arch. Hydrobiol. Suppl. 62: 333-409.

Andersen, J.M. 1976. An ignition method for determination of total phosphorus in lake sediments. Water Res. 10: 329-331.

Anderson, M.R. 1985. The relationship between sediment nutrient and aquatic macrophyte biomass in situ. Ph.D. thesis, McGill Univ.

Barko, J.W., Hardin, D.G., and M.S. Matthews. 1982. Growth and morphology of submersed macrophytes in relation to light and temperature. Can. J. Bot. 60: 877-887.

_____ , and R.M. Smart. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. J. Ecol 71: 161-175.

Baumann, P.C., A.D. Hasler, J.F. Koonce, and M. Teraguchi. 1973. Biological investigations of lake Wingra. U.S. Environmental Protection Agency Report No. R3-73-044, Washington.

Beach Erosion Board. 1972. Waves in inland reservoirs. U.S. Army Corps Eng., Beach Erosion Bd. Tech. Memo. 132.

Box, G.E.P., and P.W. Tidwell. 1962. Transformation of the independent variables. Technometrics 4: 531-540.

Breiman, L., J.H. Friedman, R.A. Olsen, and C.J. Stone. 1984. Classification and regression trees. Wadsworth.

Carpenter, S.R. 1983. Submersed macrophyte community structure and internal loading: Relationship to lake ecosystem productivity and succesion. p.p. 105-111. In J. Taggart (ed.), Lake restoration, protection, and management. U.S. E.P.A., Washington, D.C.

_______ , and M.S. Adams. 1977. The macrophyte tissue nutrient pool of a hardwater eutrophic lake: Implications for macrophyte harvesting. Aquat. Bot. 3: 239-255.

Cattaneo, A., and J. Kalff. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. Limnol. Oceanogr. 25: 280-289.

Chambers, P.A., and J. Kalff. 1985. Depth distribution and biomass of submersed macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42: 701-709.

Devol, A.H., and R.C. Wissmar. 1978. Analysis of five North American lake ecosystems. V. Primary production and community structure. Verh. Internat. Verein. Limnol. 20: 581-586.

Dillon, P.J., and F.H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767-773.

Forsberg, C. 1959. Quantitative sampling of subaquatic vegetation. Oikos 10: 233-241.

Guilizzoni, P., and C. Saraceni. 1974. Macrophyte population [In Italian], p. 183-224. In: L. Barbanti et al. (eds.), Ecological research on lago d'Endine. Ist. Ital. Idrobiol.

Hakanson, L. 1977. The influence of wind, fetch, and water depth on the distribution of sediments in lake Vanern, Sweden. Can. J. Earth Sci. 14: 397-412.

Holm, L.G., L.W. Weldon, and R.D. Blackburn. 1969. Aquatic weeds. Science 166: 699-709.

Howard-Williams, C., and B.R. Allanson. 1981. An integrated study on littoral and pelagic primary production in a south African coastal lake. Arch. Hydrobiol. 92: 507-534.

Jupp, B.P., and D.H.N. Spence. 1977a,b. Limitation of macrophytes in a eutrophic lake, Loch Leven. 1. Effects of phytoplankton. 2. Wave action, sediments and waterfowl grazing. J. Ecol. 65: 175-186, 431-446. Keast, A. 1984. The introduced aquatic macrophyte, Myriophyllum spicatum, as habitat for fish and their invertebrate prey. Can. J. Zool. 62: 1289-1303.

Landers, D.H. 1982. Effects of naturally senescing aquatic plants on nutrient chemistry and chlorophyll-a of surrounding waters. Limnol. Oceanogr. 27: 428-439.

Lind, C.T., and G. Cottam. 1969. The submersed aquatics of University Bay: A study in eutrophication. Amer. Midl. Natur. 81: 353-369.

Margalef, R. 1984. Limnologia. Omega.

Nichols, S.A. 1971. The distribution and control of macrophyte biomass in Lake Wingra. Ph.D. thesis, Univ. Wisconsin. 110 p.p.

________ . 1984. Macrophyte community dynamics in a dredged Wisconsin lake. Water Res. Bull. 20: 573-576.

Nygaard, G. 1958. On the productivity of the bottom vegetation in lake Grane Langso. Verh. Intern. Ver. Limnol. 13: 144-156.

Orloci, L. 1975. Multivariate analysis in vegetation research. Junk.

Ozimek, T. 1978. Effect of municipal sewage on the submerged macrophytes of a lake littoral. Ekol. Pol. 26: 3-39.

______ , and A. Kowalczewsk. 1984. Long term changes in the submerged macrophytes in eutrophic lake Mikolajskie (North Poland). Aquat Bot. 19: 1-11.

Pace, M. 1984. Zooplankton community structure, but not biomass influences the phosphorus-chlorophyll a relationship. Can. J. Fish. Aquat. Sci. 41: 1089-1096.

Pearsall, W.H. 1917. The aquatic and marsh vegetation of Easthwaite water. J. Ecol 5: 180-201.

Peltier, W.H., and E.B. Welch. 1970. Factors affecting growth of rooted aquatic plants in a reservoir. Weed Sci. 18: 7-9.

Prior, D.B., and J.N. Suhayda. 1979. Application of infinite slope analysis to subaqueous sediment instability, Mississippi Delta. Eng. Geol. 14: 1-10.

Richardson, F.B. 1974. Environmental analysis of the Kickapoo river impoundment. Center for Biotic systems, Institute for Environmental Studies IES Report 28. Madison, Wis.

Sain, R.S., W.J. Fonferek, M.S. Simpson, and K.W. Whittinghill. 1984. First-year vegetation following exposure of the Edmonson lake bed, Washington county, Virginia. Castanea 49: 158-166.

Sakamoto, M. 1966. Primary production in some japanese lakes and its dependance on depth. Arch. Hydrobiol. 62: 1-28.

SAS institute inc. 1982. SAS user's guide: Statistics.

Schiemer, F., and M. Prosser. 1976. Distribution and biomass of submerged macrophytes in Neusiedlersee. Aquat. Bot. 2: 3-39.

Schlott, V.G., and G. Malicky. 1984. Biomasse und Phosphorgehalt der Makrophyten in der NO-Bucht das Lunzer Untersees (Austria) in Abhangigkeit von nahrstoffreichen Zuflussen und vom sediment. Arch. Hydrobiol. 101: 265-277.

Selby, M.J. 1982. Hillslope materials and processes. Oxford.

Vollenweider, R.A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD, Paris. Technical Report DA 5/SCI/68.27.

Westlake, D.F. 1963. Comparisons of plant productivity. Biol. Rev. 38: 385-425.

Wiley, J.M., R.W. Gorden, S.W. Waite, and T. Powless. 1984. The relationship between aquatic macrophytes and fish production in Illinois Ponds: A simple model. N. Amer. J. Fish. Manag. 4: 111-119.

Wode, P.M., and J.E. Beresford. 1979. The aquatic flora of a Snowdonia lake: Llyn Gwynant. p. 87-97. In H.M. Platt (ed.), Progress in underwater science, vol. 5. Pentech.

Wholschlag, D.E. 1950. Vegetation and invertebrate life in a Marl lake. Ind. Stud. Lakes & Streams 3: 321-372.

CHAPTER III

The distribution of submerged macrophyte biomass in lakes: the contribution of littoral morphometry and water characteristics

ABSTRACT

The biomass distribution of submerged macrophytes in 25 Northeastern American lakes was studied to establish the relative contributions of lake characteristics (i.e. alkalinity, chlorophyll-a, total phosphorus, conductivity, and morphometry) and site specific characteristics (i.e. littoral slope, exposure to waves, and light levels) to the variability in submerged biomass. Lake characteristics (i.e. alkalinity) had their greatest influence over the lake average biomass of submerged macrophytes, whereas the site-specific biomass was largely a function of site conditions. Submerged macrophyte biomass decreased with increasing littoral slope and wave exposure, and increased with increasing alkalinity and light levels. The great habitat heterogeneity characteristic of the littoral zone explains the considerable variation of submerged biomass within lakes.

INTRODUCTION

Since the influence of submerged vegetation is proportional to its biomass (eg. Whitfield 1984, Canfield et al. 1983a, Smith and Adams 1986), the study of the factors that affect macrophyte biomass is an important aspect of limnology. However, the description of patterns in the biomass of submerged macrophytes is made difficult by their extreme variability within lakes (cf. Nichols 1982, Duarte and Kalff 1986) that results in large uncertainties around the average lake biomass. Furthermore, the analysis of the relationship between environmental conditions and the mean lake biomass would necessarily underepresent the influence of any factors that influence the biomass variability within lakes, such as the littoral slope. Nevertheless, the great variability of submerged biomass from lake to lake (cf. Duarte et al. 1986) suggests that whole-lake characteristics should have an important influence on submerged biomass.

The decrease in submerged biomass with increasing eutrophy and the associated reduction in water transparency (Twilley et al. 1985, Moss 1976, Ozimek and Kolwaczewski 1984) suggests trophic status and light absorption as important factors. Conversely, the ability of macrophytes to obtain their nitrogen and phosphorus requirements from the sediments (Carignan and Kalff 1980, Denny 1980, Huelbert and Gorham 1983), and the weak association between sediment levels of phosphorus and nitrogen and submerged biomass (Anderson 1978, Langeland 1982, Anderson 1985, Duarte and Kalff 1986), all suggest that the levels of these nutrients should be poorly related to submerged biomass. In contrast, the influence of the major ion chemistry of the water, particularly inorganic carbon, on the species composition (Moyle 1945, Hutchinson 1975) and biomass (Spence 1967, Wetzel and Grace 1983, Adams 1985) of submerged macrophyte communities suggests major ion chemistry as an important determinant of submerged biomass.

The relative contribution of water characteristics and littoral morphometry to the variation in submerged biomass should be a function of the level of analysis. The importance of water charateristics should be greater when the lake-average submerged biomass is studied, whereas littoral morphometry should be more important in site-specific analysis of submerged macrophyte biomass.

Here we examine the relationship between submerged biomass, lake trophic status, water chemistry, light climate, and littoral morphometry in 25 lakes. To examine the relative importance of these factors at different scales, this analysis will be done both for the lake-average biomass and for site-specific biomass estimates. Because the influence of submerged macrophytes on the littoral zone should be greatest during the period of maximum biomass, we tested our hypothesis in August. Water chemistry was represented by the total alkalinity, and electrical conductivity; lake trophic status was represented by the epilimnetic concentrations of chlorophyll-a and total phosphorus; and light levels as the percent surface irradiance received at the depth of macrophyte growth. Littoral morphometry was represented by its slope and exposure to waves.

MATERIALS AND METHODS

Macrophyte sampling

The study involved 25 lakes in Québec, New York, and Vermont, selected to cover the widest possible range in the factors studied. A method based in a relationship between plant biomass and vegetation height, derived from echosounder tracings and plant growth form (Duarte 1987) was used to measure the biomass of submerged macrophytes in August 1985. In brief, a recording echosounder (Si-tex Honda, model HE-356) was used to run six echosounding transects perpendicular to shore between a depth of c. 0.7 m and the vegetation limit, and the dominant gowth form recorded, for 187 sites. The number of sites per lake varied from 4 to 38, depending on lake size, and the range of littoral slope and exposure to wave action. The sites were selected to obtain a representation of the dominant conditions in the lake while covering the widest possible range of littoral morphometries. Lake area and mean depth were obtained from bathymetric maps, while wave exposure was estimated from the area (km^2) of open water visible at each site studied (Duarte and Kalff submitted). The height of vegetation in each transect was measured every 7-9 m from the echograms, and submerged biomass was determined from the equations in Duarte (1987). The slope of the littoral between the beginning and end of each transect was also measured from the tracings. This process resulted in more than 8000 individual estimates. To reduce this to managable proportions they were averaged over 0.5 m depth categories to yield 1400 observations, obtained from the mean of 3 to 15 individual estimates.

Limnological parameters

Epilimnetic water samples were collected with a sampling tube extended to the thermocline in the pelagic zone of each lake, or to 0.5 m of the bottom of unstratified lakes. The water was analyzed for total phosphorus following persulfate digestion (modified from Johnson 1971), and for chlorphyll-a, uncorrected for pheophytin, after filtering between 0.5 to 1 liters of water through 0.4 um Gelman membrane filters, followed by ethanol extraction (Sartory and Grobbelaar 1984) and spectrophotometric determination. Electric conductivity was measured in surface waters with a model PCM1 Cole-Parmer meter. Water transparency was measured with a 20 cm diameter Secchi disc, and the percent surface irradiance, Si, reaching the depth of growth, z, calculated as $Si = 100\ e^{-z\ k}$, where k is estimated as 1.47/Secchi (Walker 1982). The major ion chemistry of the water was obtained from published reports (Service qualite des eaux 1978, Provencher and Belanger 1979, Henson and Gruendling 1977, Lafond 1985, Long et al. 1981).

Statistical analysis

Linear regression was used to model the relationship between the environmental factors and submerged biomass. The dependent and independent variables were transformed when necessary to meet requirements of linear regression, and the reduction in mean square error (MSE) used to choose between alternative models. Where needed, the data were split into groups to minimize the MSE (Breiman et al. 1984, Duarte and Kalff 1986).

RESULTS AND DISCUSSION

The lakes are of glacial origin, with the exception of a single reservoir (L. Boivin). Their catchments vary from totally forested and unaffected by human influence (e.g. L. Cromwell, L. Montjoie), to lakes that support some recreational use (e.g. L. George, L. Memphremagog), and lakes heavily influenced by sewage inputs (e.g. L. Boivin, L. Waterloo). The lakes covered wide ranges in morphometric and environmental conditions (Table 1), ranging in size from the large Missisquoi Bay (L. Champlain), to lakes less than a hectare in surface (L. Cromwell). The lakes also varied from highly oligotrophic (e.g. L. George, L. Bowker), to highly eutrophic (e.g. L. Boivin, L. Waterloo, Table 1). The smallest ranges were those for total alkalinity and electrical conductivity (Table 1), reflecting the dominance of igneous and metamorphic geologies in Northeastern North America. The lakes also differed in their light absorption characteristics from lakes where light extinction is largely a function of algal biomass (e.g. L. Memphremagog), to highly coloured lakes (e.g. L. Cromwell); this is reflected in the relatively poor relationship between chlorophyll-a concentration and Secchi depth in these data (r^2=0.51). A wide range of taxonomic compositions (Table 1) was also represented in the submerged vegetation of the lakes studied.

The littoral of the lakes ranged from very steep (eg. L. Bowker, L. Brompton, Table 2), to very gentle (e.g. L. Selby, Roxton Pond, Table 2), some lakes presenting a wide diversity of slopes (e.g. L. George, Table 2). Given the differences in littoral slope among lakes (Table 2), littoral slope appears to be as much a characteristic of the lakes as it is a property of specific sites. The exposure to waves covered a wide range, but had little variation within lakes (Table 2) because it is largely a function

Table 3.1 Limnological characteristics of the lakes studied, range of macrophyte biomass, and dominant species.

Lake	Lat.	Long.	Area	Zmax	Zm
Bleu	45 55	73 56	1.3	6	-
Boivin	45 23	72 45	160	6	1.6
Bowker	45 25	72 13	230	59	25.9
Brome	45 15	72 30	1452	12.77	5.8
Brompton	45 26	72 09	1191	42.3	11.5
Missisquoi Bay	45 03	73 09	7750	4	2.8
Conneley	45 54	73 58	129.4	21.9	7.72
Croche	45 54	73 10	9.1	10.5	8.5
Cronwell	45 59	73 09	4.8	18	3.04
D'Argent	45 18	72 18	96	15.5	4.6
George	43 30	73 40	11000	59	18
Hertel	45 32	73 09	29	8.3	4.8
Lovering	45 10	72 09	464	24.9	10.3
Magog	45 15	72 10	1080	19.2	9.8
Massawippi	45 13	72 00	1790	85	40.2
Memphremagog	45 14	72 14	9010	108	18
Montjoie	45 24	72 05	329	22.2	7.9
Orford	45 18	72 16	122	48	17.7
P. Brompton	45 26	72 06	67	19.5	7.5
Roxton pond	45 28	72 39	179	5.47	3.16
Selby	45 53	72 47	111	8	2.6
Silver	45 38	72 48	67.8	61.6	27
Stukely	45 22	72 15	386	32.2	13.6
Trousers	45 14	72 20	59.57	13	7.2
Waterloo	45 20	72 05	150	4.9	2.9

Area in ha, maximum (Zmax) and mean depth (Zmean) in m, conductivity (C) in µS cm^{-1}, alkalinity (Alk) in mg $CaCO_3$ l^{-1}, Secchi depth in m, total phosphorus (TP) in mg m^{-3}, and chlorophyll-a in mg m^{-3}. P. = *Potamogeton*, M. = *Myriophyllum*, E. = *Elodea*, V. = *Vallisneria*, I. = *Isoetes*.

Table 3.1 (Cont.)

Lake	C	Alk	Secchi	Chl-a	TP	D. sp.
Bleu	35	7.2	4.2	-	-	P. foliosus
Boivin	321	78	0.6	15.2	125	M. spicatum
Bowker	47.6	18.2	7.8	0.99	9.8	P. robinsii / I. lacustris
Brome	89	32.3	3.7	2.04	13.1	V. americana
Brompton	59	21.7	4.2	1.25	2.7	P. praelongus
Missisquoi Bay	94.3	26.7	1.8	10	65	M. spicatum
Conneley	95.5	21.6	5.14	1.49	9.21	P. praelongus
Croche	29	8.53	3.98	1.65	9.92	-
Cronwell	35.1	9.83	2.39	8.63	11.47	P. praelongus
D'Argent	87	31.1	3.1	3.5	14.5	M. spicatum / P. praelongus
George	90	24	8.5	0.95	8.5	M. spicatum / P. amplifolious
Hertel	86	50	3.8	3	9.8	P. perfoliatus / P. robinsii
Lovering	56.7	23.6	2.8	2.1	16	M. exalbescens / Nitella sp.
Magog	165	50.4	2.5	9.3	39.5	M. spicatum / E. canadensis
Massawippi	140	70	4.5	4.6	16.25	M. spicatum
Memphremagog	145	45	4	6.8	9	M. spicatum / P. robinsii
Montjoie	36	18.1	3.2	0.84	8.5	P. foliosus
Orford	226	39.8	8	0.55	1.09	P. praelongus
P. Brompton	63.1	27.7	3.6	1.95	6	V. americana / I. lacustris
Roxton pond	120	39	2.9	4.1	18	M. spicatum
Selby	160	49	2.7	7.2	10.8	M. spicatum
Silver	110	35	5.8	3.51	8.3	E. canadensis
Stukely	49	24.3	6.5	0.84	2.9	P. perfoliatus
Trousers	55	14.6	2	1.1	7	P. species
Waterloo	148.9	44.1	0.77	23.7	34.2	M. spicatum /V. americana

Table 2. Mean and coefficient of variation of the biomass, slope, and wave exposure in the littoral of the different lakes.

Lake	Slope		Exposure	
	Mean	C.V.	Mean	C.V.
Bleu	14.93	88.1	0.077	44.2
Boivin	6.92	166.3	0.36	38.9
Bowker	41.2	76.0	0.16	87.5
Brome	2.83	39.2	11.62	15.6
Brompton	20.21	48.1	0.21	20.0
Brompton	5.19	115.6	7.62	36.0
Conneley	17.61	145.4	0.73	25.8
Croche	20.78	37.4	0.39	0.3
Cromwell	9.15	40.4	0.11	1.8
D'Argent	12.02	101.7	0.86	2.2
George	7.47	139.0	18.46	84.1
Hertel	3.58	91.6	0.28	3.2
Lovering	4.12	78.4	2.55	80.0
Magog	2.37	50.6	3.19	44.8
Massawippi	4.86	110.9	5.44	59.9
Memphremagog	8.27	76.9	11.17	94.4
Missisquoi B.	2.56	66.8	42.9	43.1
Montjoie	9.18	63.2	3.29	0.6
Orford	5.71	51.5	0.71	64.8
Roxton P.	1.47	33.3	2.6	0.5
Selby	2.19	27.8	0.39	0.8
Silver	13.15	66.1	0.57	33.3
Stukely	7.96	83.2	1.45	33.6
Troussers	16.19	56.0	0.085	75.3
Waterloo	2.77	130.3	0.7	34.2

Slope in %, exposure in Km, and biomass in g. fresh wt. m^{-2}.

Table 3.2 (Cont.)

Lake	Biomass	
	Mean	C.V.
Bleu	5	10.6
Boivin	300	326
Bowker	10	22.9
Brome	42	25
Brompton	2	3.8
Brompton	23	230
Conneley	116	176
Croche	0	0
Cromwell	50	117
D'Argent	138	155
George	114	166.8
Hertel	504	494
Lovering	40	44.1
Magog	439	323
Massawippi	514	684
Memphremagog	206	229
Missisquoi B.	89.8	86.8
Montjoie	1	2.02
Orford	72	47
Roxton P.	606	168
Selby	1113	141
Silver	45	78
Stukely	10	18.4
Troussers	8	16
Waterloo	212	282

of lake size ($r = 0.90$). The diversity in littoral and lake conditions was matched by the great variation in submerged biomass both among and within lakes (Table 2). The variance in biomass in some lakes (e.g. L. Massawippi, Table 2) is as large as the overall variance, suggesting that the factors that determine the variation in biomass within lakes must be at least as important as those that influence the lake averages. This idea is supported by the possitive correlation between the variability in submerged biomass within lakes (as the coefficient of variation) and the corresponding variability in littoral slope ($r = 0.45$, $P < 0.01$).

Lake-average biomass

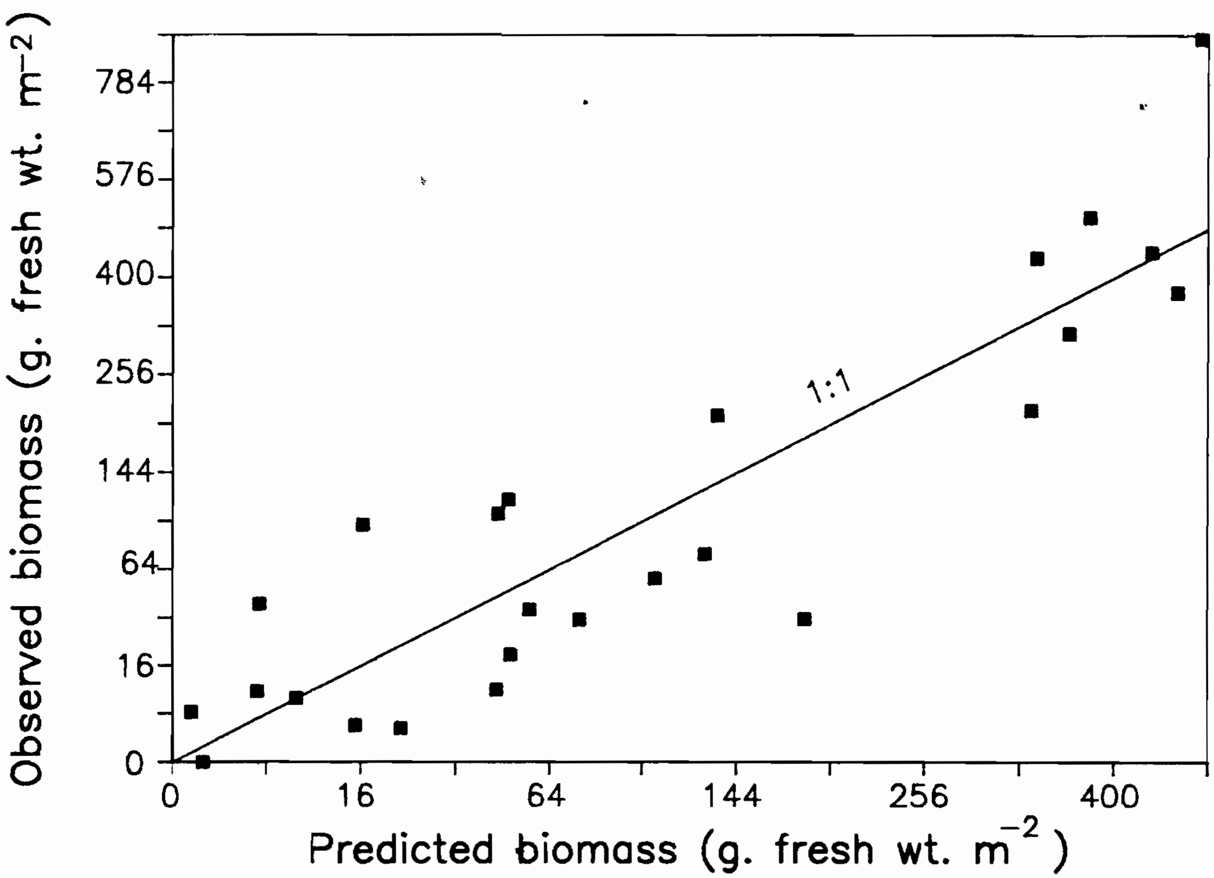
The lake-average biomass of submerged macrophytes, approximated as the average of all biomass estimates (N = 54 - 280), is important to determine their relative influence on the littoral of the lakes. These values were strongly correlated with the average littoral slope and with water alkalinity, which is an index of the availability of dissolved inorganic carbon (Fig. 1). The best model to describe these relationships is:

$$\text{biomass}^{0.5} = -2.2 - 0.6\ \text{slope}^{-0.81} + 0.8\ (\text{alkalinity/slope})^{0.5} \qquad (1)$$

$$r^2=0.80;\ P < 0.0001;\ S.E._{(\text{estimate}^{0.5})} = 3.7$$

where biomass is measured in g. fresh wt. m^{-2}, slope as the depth change in m per m of horizontal distance, and alkalinity in mg l^{-1} as $CaCO_3$. The interaction term in the model (Eq. 1) indicates that the positive relationship of submerged biomass and alkalinity is modulated by the littoral slope. If the positive relationship to alkalinity is interpreted as suggesting carbon limitation of submerged biomass, then the interaction term suggests that the stress that the plants experience in lakes with steep slopes, reduce their ability to respond to increasing concentrations of inorganic carbon.

Figure 3.1 The relationship between the lake-average biomass of submerged macrophytes and that predicted from alkalinity and the average slope (Eq. 1).



Submerged biomass is positively correlated to lake trophic status (as chlorophyll-a, $r = 0.58$, $P < 0.05$). However, this correlation is no longer significant after littoral slope is considered indicating that the idea that heavy submerged growth is an indication of cultural eutrophication (e.g. Lind and Cottam 1969) may be the result of eutrophic lakes often having gentle slopes, larger sediment loadings, and hard waters. The weak correlation between littoral slope and mean depth ($r = 0.39$, $P < 0.05$), explains that submerged biomass is not clearly related to lake depth (e.g. Duarte et al. 1986).

Total alkalinity often correlates well with total phosphorus or conductivity, so that the interpretation of the relationship between submerged macrophytes and alkalinity is often ambiguous (cf. Hutchinson 1975). However, the relationship between biomass and alkalinity ($r = 0.80$, $P < 0.001$) is statistically stronger than those to total phosphorus ($r = 0.40$, $P < 0.05$) or conductivity ($r = 0.72$, $P < 0.01$). Further, the partial correlation of submerged biomass to alkalinity (after considering littoral slope) is highly significant ($P < 0.001$), whereas those to total phosphorus and conductivity are not ($P > 0.05$). The relatively low correlation between conductivity and alkalinity ($r^2 = 0.57$) in our lakes reflect the influence of road salt on five of the 25 lakes studied (Table 3). This is evident in their high Cl/K ratios (Table 3) compared to 5.71 (by weight), the characteristic ratio for North American waters (Livingstone 1963).

Since the proportions of most major ions are fairly constant in freshwaters (Rodhe 1949), regression analyses are unlikely to discriminate the observed relationship between biomass and alkalinity from a possible relationship to ions unaffected by salting, such as potassium or calcium.

Table 3.3 Ratio of chloride to potassium by weight for the five lakes affected by road salting, and the typical ratio for North American waters (Livingstone 1963)

Lake	Cl/K
Brome	16.2
D'Argent	18.1
Conneley	26.8
Orford	49.9
Waterloo	16.0
North America	5.7

The confounding correlations of total alkalinity to these ions have been resolved experimentally by Martin et al. (1970), who showed inorganic carbon to be most directly involved in a similar relationship between alkalinity and the yield of Najas sp. Limitation of submerged biomass by potassium or calcium may also be prevented by their ability to obtain both these nutrients from the sediments (DeMarte and Hartman 1974, Martin et al. 1970, Waisel et al. 1982, Huebert and Gorham 1983), although the relative contributions of these two elements by sediment and water sources are unknown. Sediment carbon is not widely used by macrophytes because this requires specialized root systems only found in a few soft-water rosette species (Wium-Andersen 1971, Sand-Jensen and Sondergaard 1978, Sondergaard and Sand-Jensen 1979, Loczy et al. 1983), so that most macrophytes species obtain carbon from the water.

The limitation of submerged biomass by carbon has been proposed on theoretical grounds (Spence 1967, Hutchinson 1975, Spence 1982, Wetzel and Grace 1983, Adams 1985, Barko et al. 1986), based on the very slow diffusion of CO_2 in water and the relatively large boundary layers that surround macrophyte leaves (Black et al. 1981, Madsen 1984). More indirect evidence for the role of alkalinity comes from work in several Florida lakes where submerged macrophyte removal by grass carp was followed by highly significant increases in water alkalinity (Canfield et al. 1983b, Small et al. 1985). Diurnal depressions of inorganic carbon (e.g. Pokorny et al. 1984), and raise in pH (Goulder 1970) are often observed in connexion to submerged plant photosynthesis. Additionally, Goulder (1969) demonstrated a strong spatial correlation between submerged macrophyte cover and total alkalinity in a pond with patchy vegetation.

Depth- and site-specific plant biomass

The study of the mean biomass of macrophytes across entire lakes treats their variability within the lakes as error around this mean, whereas it may be related to habitat heterogeneity around the littoral zone (Duarte and Kalff 1986). Consequently, the relationship between submerged biomass and factors that vary around the littoral, such as the light levels reaching the plants, the exposure to waves, and the littoral slope, would be better represented by a site-specific analysis than by the examination of the average biomass.

The biomass of submerged plants varied regularly with depth, following a dome-shape profile in all lakes (Figure 2). This distribution suggests limitation by wave exposure at shallow depths and by light limitation below the depth of maximum biomass (Spence 1982). The shape of the depth/biomass curve is strongly related to the water transparency, since both the depth of maximum colonization (Zmc) and the depth where the maximum biomass occurs (Zmb) are functions of the water transparency (Figure 3):

$$\text{Zmc (m)} = 1.9 + 0.63 \text{ Secchi (m)} \quad (r^2 = 0.76,\ P < 0.0001) \qquad (2)$$

$$\text{Zmb (m)} = 1.1 + 0.4 \text{ Secchi (m)} \quad (r^2 = 0.79,\ P < 0.0001) \qquad (3)$$

These relationships are stronger than those previously reported (Chambers and Kalff 1985, Canfield et al. 1985), likely because the large number of transects examined within each lake reduces the uncertainty around the average estimates, which in this case is similar to the error around the regression estimates. The depth/biomass profile is also determined by the shallowest depth where submerged vegetation grows (0.75 - 1.25 m). However, this minimum depth is not related to slope, exposure or transparency ($P > 0.05$), suggesting that the shallow limit is probably set by ice scouring which similarly erodes the sediments of the shallowest areas in all these

Figure 3.2 The depth profile of submerged macrophyte biomass in the lakes studied constructed by pooling together the data for all sites.

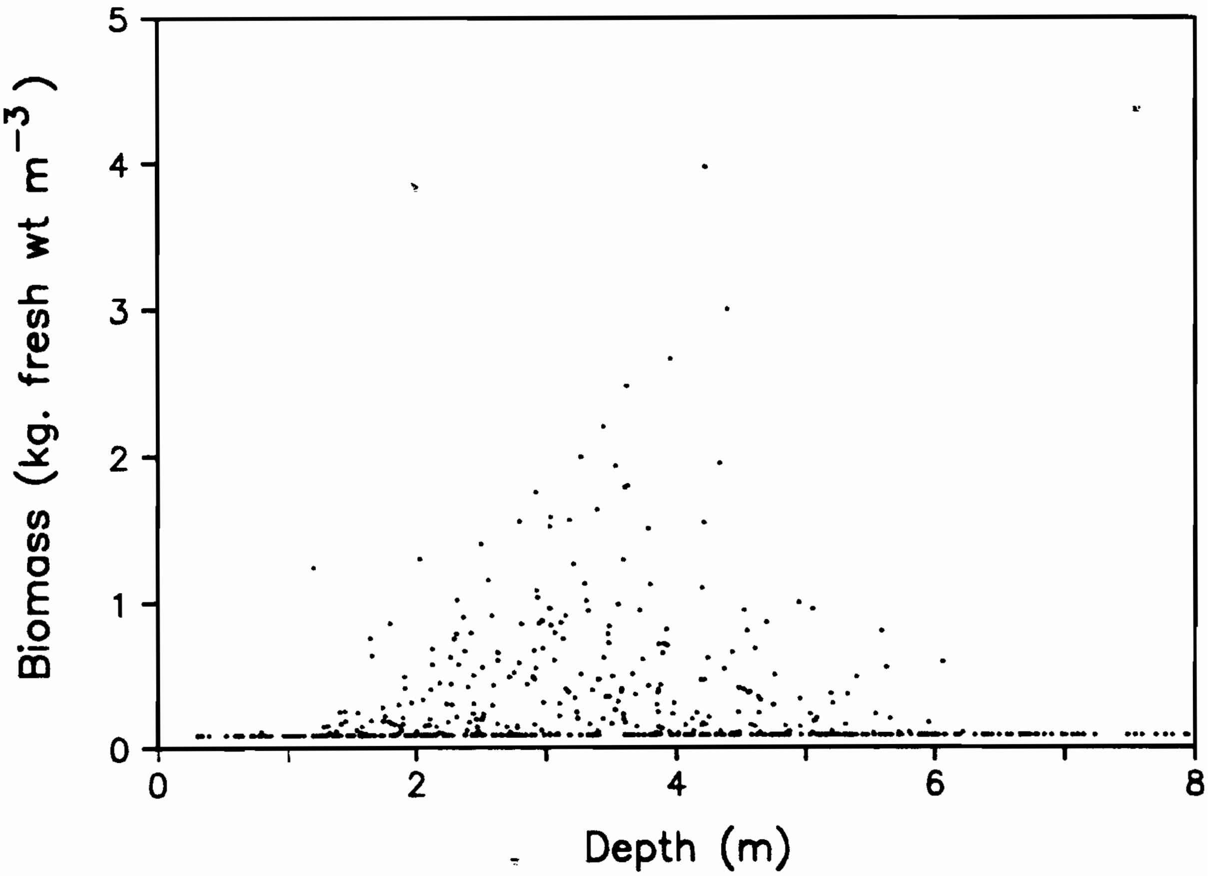
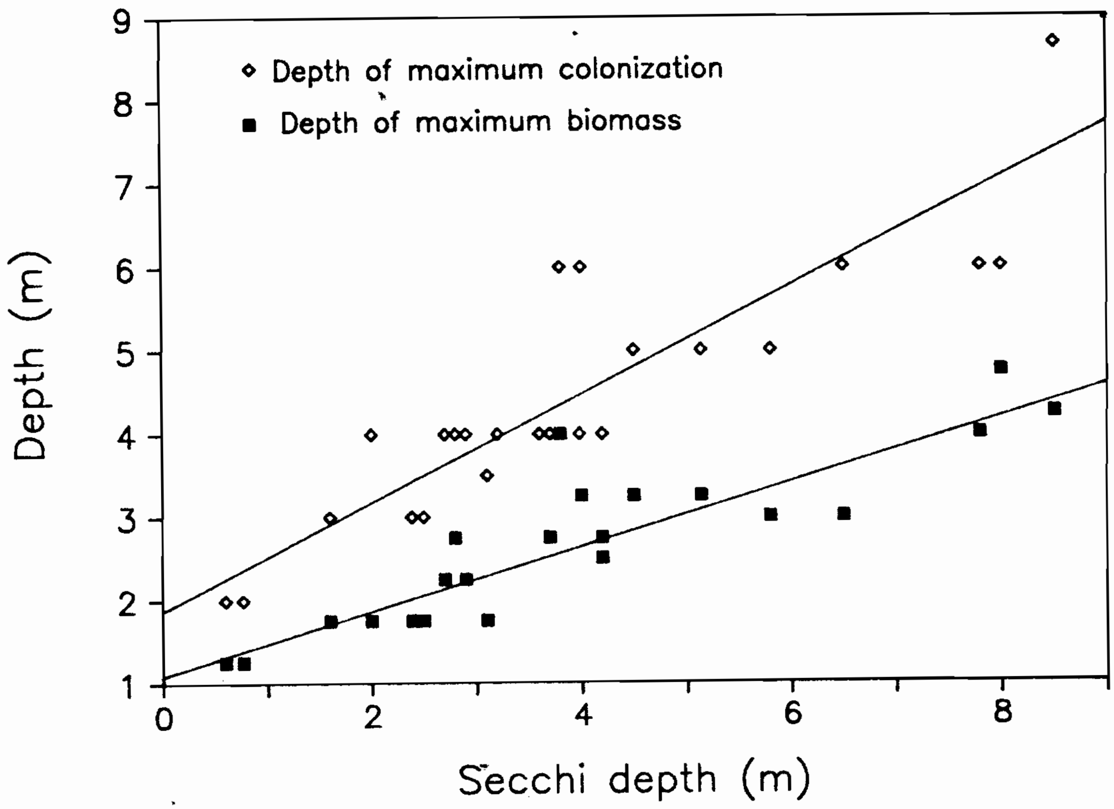


Figure 3.3 The relationships between the depth of maximum colonization (Zmc, Eq. 2) and the depth of maximum biomass (Zmb, Eq. 3) of submerged macrophytes and the water transparency of the lakes studied.



lakes.

We attempted to describe the precise distribution of biomass in the different sites by regression analysis using lake and site characteristics as independent variables. However, this analysis resulted in a model with over 12 highly significant ($P<0.0001$) terms, explaining in total some 40% of the variance. Such a model is unsatisfactory because of its complexity, and because the effect of individual factors is difficult to extract from the conglomerate of simultaneous changes and interactions. The complexity of the model must reflect the changing importance of the different environmental factors with depth. This is further evident when the variation in the partial correlation coefficients between submerged biomass and the different variables are presented as a function of depth (Fig. 4). While the correlations to littoral slope and alkalinity remain relatively constant at all depths, Secchi transparency shows stronger correlations at greater depths, and exposure at shallower depths (Fig. 4).

Because the complexity of these interactions makes linear regression models cumbersome, we chose to simplify the model by exploring the data further. Since submerged biomass is zero when slopes are steep (Fig. 5), we believe that a critical slope exists beyond which plants will not grow. This critical slope was found to be about 14.8% (Fig. 5), as calculated by the technique proposed by Breiman et al. (1984). The division of the data into two sets at this critical slope reduced the overall variance by 13% (F-test, $P<0.0001$). In one set the submerged biomass would be 0 due to steep slopes ($N = 302$), and the other could be subjected to further analysis ($N = 1098$). This second set could also be divided, on the basis of the relationship between the maximum depth of colonization and the Secchi transparency (Eq. 2, Fig. 3), between locations where plant growth is

Figure 3.4 The change in the partial correlations of slope, exposure, transparency, and alkalinity to macrophyte biomass with depth. N > 70 for all correlations. Numbers in the left indicate probability levels.

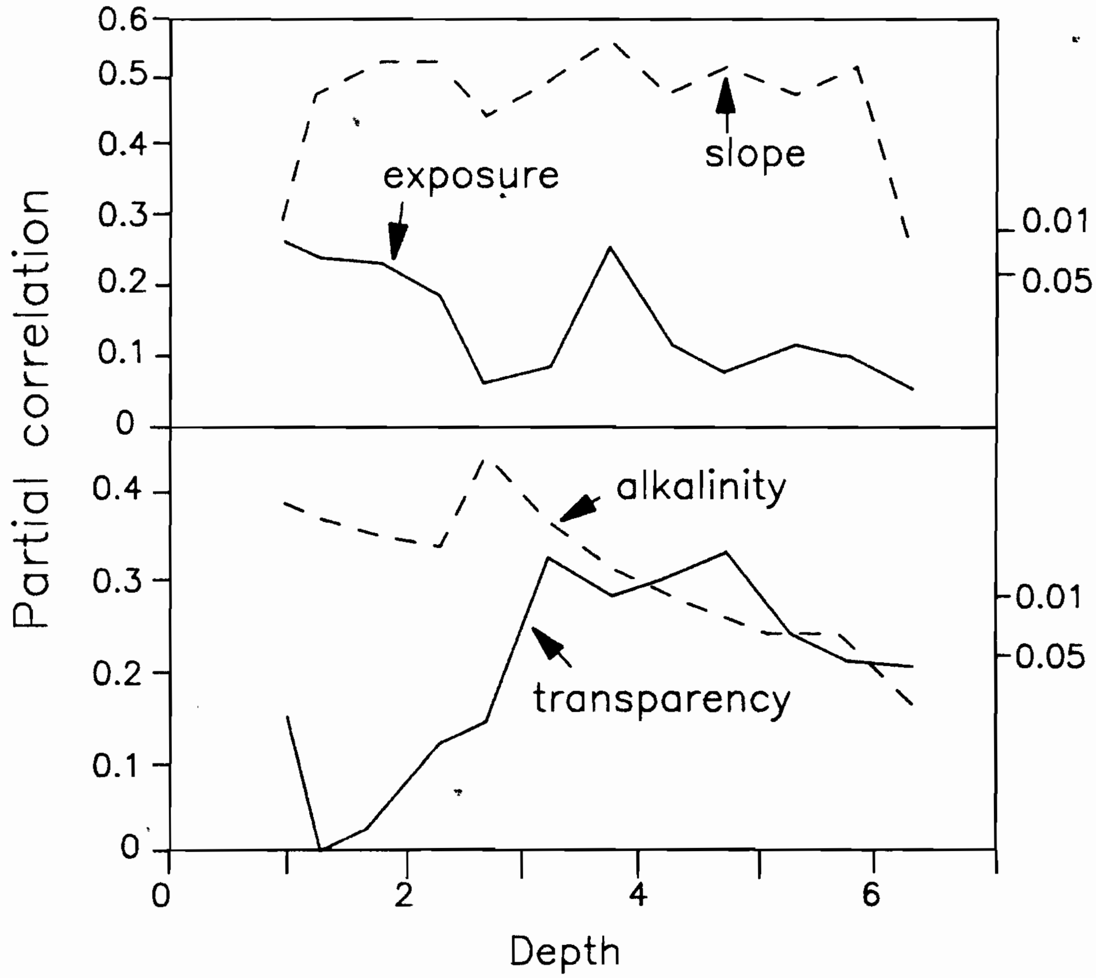
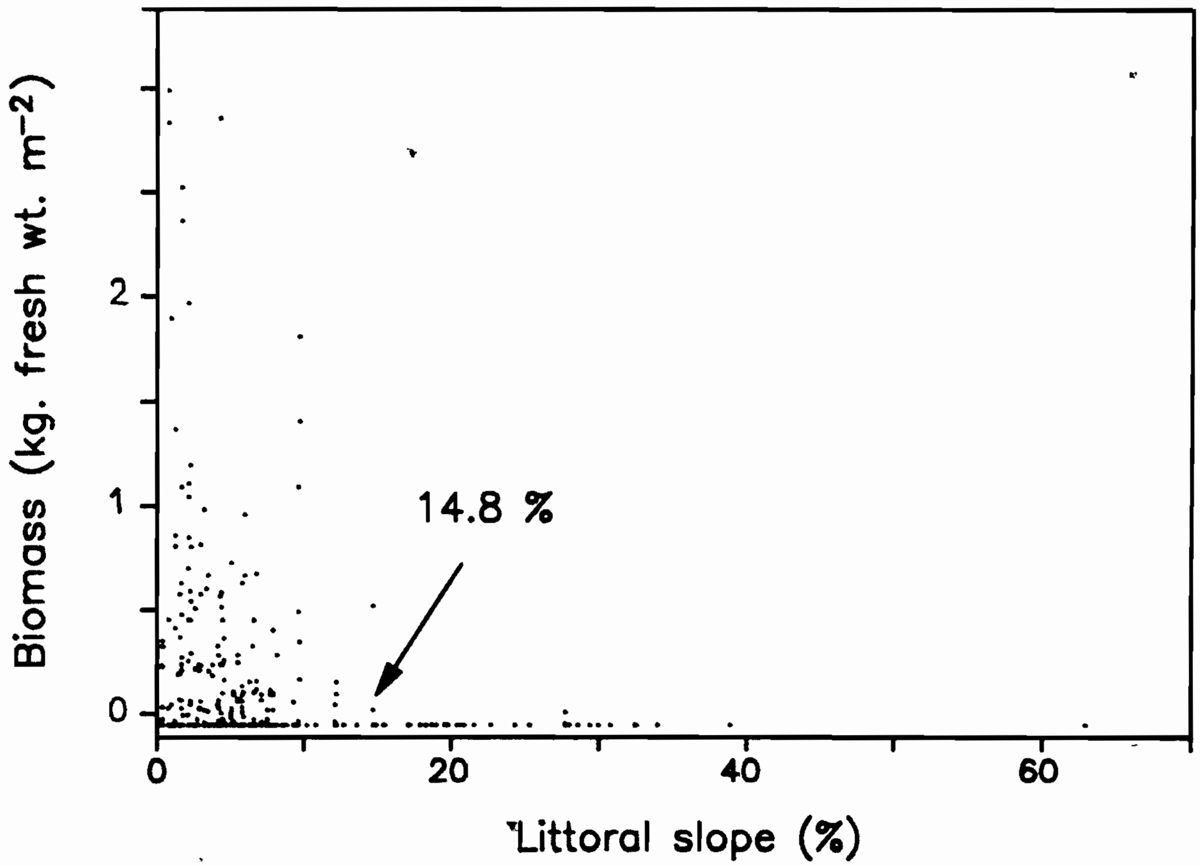


Figure 3.5 The relationship between littoral slope and the biomass of submerged macrophytes showing the value of the critical slope above which plants do not grow.



prevented by light limitation and those where plant growth can occur. This separation indeed explained a further 9% of the total variance (F test, $P<0.0001$).

The differences in the importance of wave exposure and water transparency for shallow and deep locations (Fig. 4), suggests that the observations in areas with slopes lower than 14.8 and shallower than the maximum depth of colonization (where some plant growth may occur) can be divided into two subgroups based on the depth of maximum biomass and the Secchi transparency (Eq. 3, Fig. 2). In locations deeper than the depth of maximum biomass, light levels should play an important role, whereas in the shallower locations the light regime should be less critical, and wave exposure should play a significant role. The multiple regressions resulting from these data sets confirmed the suspected differences in the relationships between submerged biomass and environmental factors over the two depth ranges:

The best regression model for the data set containing locations deeper than the depth of maximum biomass (calculated from Eq. 3) is:

$$\text{biomass}^{0.33} = -13.0 - 1.6 \ln \text{slope} - 0.45 \ln \text{exposure} + 2.3 \ln \text{alkalinity} + 1.2 \ln \text{Si} \quad (4)$$

$$r^2 = 0.31;\ P < 0.0001,\ \text{S.E.}_{(\text{estimate}^{0.33})} = 3.1$$

where Si is the percent surface irradiance received at the depth of growth, exposure is measured in Km^2, and the units for other variables are similar to those in Eq. 1. This equation supports the postulated influence of light levels in limiting biomass below the depth of maximum biomass. It also indicates that increasing slope and exposure, and decreasing alkalinity results in lower biomass values.

The shallow water model confirms the importance of slope, alkalinity and wave action:

$$\text{biomass}^{0.33} = -\,8.4 - 1.6\ \ln \text{slope} - 0.3\ \ln \text{exposure} + 2.0\ (\text{alkalinity*depth})^{0.33} \qquad (5)$$

$$r^2 = 0.40;\ P<0.0001;\ S.E._{(\text{estimate}^{0.33})} = 2.6$$

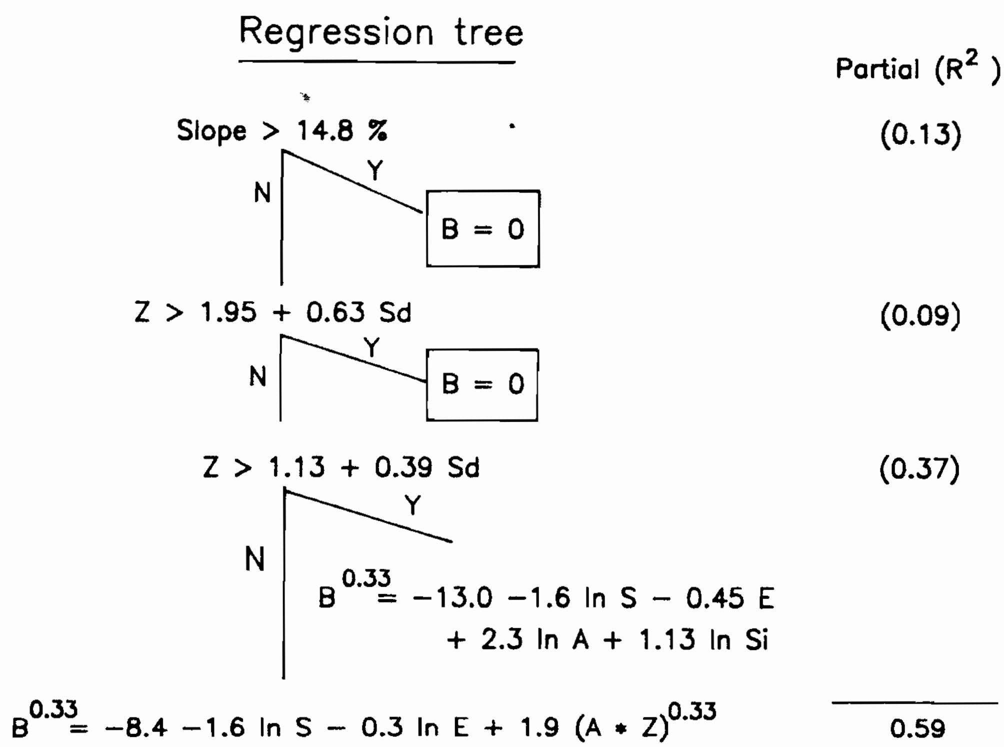
The coefficients for the littoral slope are similar in both deep and shallow water models (slope= 1.6, Eqs. 4 and 5). However, plant biomass appears paradoxically less influenced by exposure in the shallow model (slope = 0.3) than in the deep water model (slope = 0.45). At the same time, the model shows a positive relationship between biomass and depth, this being more important at high alkalinities where biomass is greater. This interaction cannot be attributed to the attenuation of wave energy with increasing depth, because the interaction term for exposure and depth was not significant ($P>0.05$). While Duarte and Kalff (submitted) found a direct negative influence of wave action on the response of submerged plants to nutrient additions at the depth of maximum biomass (2.5 m), they were unable to demonstrate this link for shallower (1.0 m) plants. They concluded that erosion due to ice scouring may be more important than wave action in reducing the biomass of the shallow plants. In lakes with higher alkalinity, whose biomass is greater, the increase in biomass with depth may also reflect limitation by the underwater space available for growth in shallow sites (Lind and Cottam 1978). Whatever the relative roles of ice scouring and space limitation, our results suggest that the importance of wave action in controlling submerged biomass in shallow waters may have been exaggerated in the past (Jupp and Spence 1977, Spence 1982). Since the relative importance of single extreme wind events compared to continuated wave action, and the relative influence of wind events at different stages of plant growth are unknown, the weak relationship between exposure and plant biomass may also indicate that standard measures of exposure, such as the exposure area used here or the weighted fetch method (see Duarte and Kalff 1986), fail to measure the scale of relevance.

The data reduction steps described can be combined in a "regression tree" (sensu Breiman et al. 1984, Fig. 6), where the predicted biomass is obtained by following the tree until a terminal branch is reached (Fig. 6). The model is simpler than a 12 term regression model, and allows for a more clear stepwise representation of the factors affecting submerged biomass, the total model accounting for almost 60% of the variance in depth- and site-specific submerged biomass. The large unexplained variance in this models is not unexpected, because submerged weedbeds are very patchy (Downing and Anderson 1985), and suggests that these relationships should be improved by considering variables that reflect habitat heterogeneity and differences in community structure.

Limnological implications

The strong relationship of mean submerged biomass to alkalinity and littoral slope bears some resemblance to the Morphoedaphic Index (total dissolved solids/mean depth), proposed as a predictor of fish production in lakes (Ryder 1964). This index summarizes two basic patterns in comparative limnology. First, a positive correlation between total dissolved solids (and its correlates) and productivity (Gorham et al. 1974, Prepas 1983), and secondly a negative relationship between lake morphometry and productivity proposed many times in the past (Rawson 1955, Sakamoto 1966, Straskraba 1980). Although the mechanisms that link the morphoedaphic index to the productivity of fish likely differ from those resulting in greater macrophyte biomass, the similarity in the patterns for fish and macrophytes is consistent with the positive relationship between submerged vegetation and fish abundance in lakes (Whitfield 1984).

Figure 3.6 Regression tree describing the relationship between the site and depth specific biomass of submerged macrophytes to environmental conditions.



The relationship between submerged biomass and alkalinity adds to the evidence pointing to its influence on the community structure (Moyle 1945, Seddon 1972, Hutchinson 1975, Pip 1979, Hellquist 1980), species richness (Cattling et al. 1986), and productivity (Adams et al. 1982) of submerged vegetation to highlight the major role of carbon on macrophyte ecology. The abundant evidence for carbon limitation of submerged biomass contrasts with the scarcity of similar evidence for phytoplankton (Schindler 1977, but see Talling 1976). This difference may derive from the much lower turnover rate of macrophytes, so that carbon limitation of photosynthetic rates (Adams et al. 1978) can reduce the biomass macrophytes accummulate throughout the summer, even if this situation only occurs sporadically. Additionally, phytoplankton cells are being mixed throughout the epilimniom, present boundary layers many times smaller than those associated with macrophyte tissues (Black et al. 1981), and are more able to use bicarbonate, hence benefiting from a much more efficient supply of dissolved inorganic carbon (Spence and Maberly 1985).

Conclusions

We have shown here that the relative contribution of site (slope, exposure, light levels and depth) and lake (alkalinity, average slope) characteristics to the biomass of submerged macrophytes depends on the scale of analysis. While lake characteristics are more important when comparing the lake-average submerged biomass, the variability within lakes is largely a function of site specific characteristics, and ultimately of the complexity of their littorals. This explains why general morphometric features, such as mean depth, are weaker descriptors of submerged biomass (Duarte et al. 1986) than of the biota inhabiting the more homogeneous pelagic environment (Rawson 1955, Sakamoto 1966). Because of the great diversity of the littoral zone, we suggests that studies of the relationship of submerged macrophytes, and their associated biota, and their environment should be focussed on site specific, rather than on whole-lake studies.

REFERENCES

Adams, M.S. 1985. Inorganic carbon reserves of natural waters and the ecophysiological consequences of their photosynthetic depletion: II. Macrophytes. pp 421-435. In W.J. Lucas and J.A. Berry (eds.). Inorganic carbon uptake by aquatic phototosynthetic organisms. The American Society of Plant Physiologists, Baltimore, USA.

_______ , S. Guilizzoni, and S. Adams. 1978. Relationship of dissolved inorganic carbon to macrophyte photosynthesis in some Italian lakes. Limnol. Oceanogr. 23: 912-913.

Anderson, M.G. 1978. Distribution and production of sago pondweed (Potamogeton pectinatus L.) on a Northern prairie marsh. Ecol. 59: 154-160.

Anderson, M.R. 1985. The relationship between sediment nutrients and aquatic macrophyte biomass in situ. Ph.D. thesis, McGill University, Montreal.

Barko, J.W., M.S. Adams, and N.L. Clesceri. 1986. Environmental factors and their consideration in the management of submerged aquatic vegetation: a review. J. Aquat. Plant Manage. 24: 1-10.

Black, M.A., S.C. Maberly, and D.H.N. Spence. 1981. Resistance to carbon dioxide fixation in four submerged freshwater macrophytes. New Phytol. 89: 557-568.

Breiman, L., J.H. Friedman, R.A. Olsen, and C.J. Stone. 1984. Classification and regression trees. Wadsworth.

Canfield, D.E., Jr, K.A. Langeland, M.J. Maceina, W.T. Haller, and J.V. Shireman. 1983a. Trophic state classification of lakes with aquatic macrophytes. Can J. Fish. Aquat. Sci. 40: 1713-1718.

______ , M. J. Maceina, and J. V. Shireman. 1983b. Effects of Hydrilla and grass carp on water quality in a Florida lake. Water Resour. Bull. 19: 773-778.

______ , K. A. Langeland, S.B. Linda, and W.T. Haller. 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. J. Aquat. Plant Manage. 23: 25-28.

Carignan, R., and J. Kalff. 1980. Phosphorus sources for aquatic weeds: water or sediment? Science 207: 987-989.

Cattling, P.M., B. Freedman, C. Stewart, J.J. Kerekes, and L.P. Lefkovitch. 1986. Aquatic plants of acid lakes in Kejimkujik National Park, Nova Scotia; floristic composition and relation to water chemistry. Can. J. Bot. 64: 724-729.

Chambers, P.A., and J. Kalff. 1985. Depth distribution and biomass of submerged macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42: 701-709.

DeMarte, J.A., and R.T. Hartman. 1974. Studies on absorption of ^{32}P, ^{59}Fe, and ^{45}Ca by water milfoil (Myriophyllum exalbescens, Fernald). Ecology 55: 188-194.

Denny, P. 1980. Solute movement in submerged angiosperms. Biol. rev. 55: 65-92.

Duarte, C.M. 1987. The use of echosounding tracings to estimate the aboveground biomass of submerged macrophytes. Can. J. Fish. Aquat. Sci. 44: In press.

_______ , and J. Kalff. 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnol. Oceanogr. 31: 1072-1080.

_______ , _______ , and R.H. Peters. 1986. Patterns in the biomass and cover of aquatic macrophytes in lakes. Can. J. Fish. Aquat. Sci. 43: 1900-1908.

Downing, J.A., and M.R. Anderson. 1985. Estimating the standing biomass of aquatic macrophytes. Can. J. Fish. Aquat. Sci. 42: 1860-1869.

Gorham, E, J.W.G. Lund, J.E. Sanger, and W.E. Dean, Jr. Some relationships between algal standing crop, water chemistry, and sediment characteristics in the English Lakes. Limnol. Oceanogr. 19: 601-617.

Goulder, R. 1969. Interactions between the rates of production of a freshwater macrophyte and phytoplankton in a pond. Oikos 20: 300-309.

________ . 1970. Day-time variations in the rates of produccion by two natural communities of submerged freshwater macrophytes. J. Ecol. 58: 521-528.

Hakanson, L. 1977. The influence of wind, fetch, and water depth on the distribution of sediments in Lake Vanern, Sweden. Can. J. Earth Sci. 14: 397-412.

Hellquist, C.B. 1980. Correlation of alkalinity and the distribution of Potamogeton in New England. Rhodora 82: 331-344.

Henson, E.B., and G.K. Gruendling. 1977. The trophic status and phosphorus loadings of Lake Champlain. EPA - 600/3-77-106. Corvallis, Oregon. 141 pp.

Huebert, D.B., and P. R. Gorham. 1983. Biphasic mineral nutrition of the submersed aquatic macrophyte Potamogeton pectinatus l. Aquat. Bot. 16: 269-284.

Hutchinson, E.G. 1975. A treatise on limnology. III. Wiley.

Johnson, D.L. 1971. Simultaneous determination of arsenate and phosphate. Env. Sci. Tech. 5: 411- 414.

Lafond, M. 1985. Biocenose et production du nannoplankton au class de tiery dans dix lacs du buclier canadien: relation avec la transparence de l'eaux. M.Sc. thesis, Universite de Montreal. 99 p.p.

Langeland, K.A. 1982. Relationships among hydrosoil, water chemistry, transparency, chlorophyll-a and submersed macrophyte biomass. Ph.D. dissertation, University of Florida, Gainesville, Florida.

Lind, C.T., and G. Cottam. 1969. The submerged aquatics of University Bay: A study in eutrophication. Am. Midl. Nat. 81: 353-369.

Livingstone, D. A. 1963. Chemical composition of rivers and lakes. Geol. Survey Profess. Papers, 440-G. U.S. Govn. Print. Off., Washington.

Loczy, S., R. Carignan, and D. Planas. 1983. the role of roots in carbon uptake by the submerged macrophytes Myriophyllum spicatum, Vallisneria americana, and Heteranthera dubia. Hydrobiologia 98: 3-7.

Long, D.R., L. Eichler, D.A. Roberts, T.C. Ryan, D.B. Shafer, J. Schaminger, K.L. Smith, and D.H. Pope. 1981. The Lake George monitoring program for the year April 1980 - April 1981. p.p. 53-82. In: C.W. Boylen (Ed.), The Lake George ecosystem. The Lake George Association, New York.

Madsen, T.V. 1984. Resistance to CO_2 fixation in the submerged aquatic macrophyte Callitriche stagnalis Scop. J. Exper. Bot. 35: 338-347.

Martin, J.B., B.N. Bradford, and H.G. Kennedy. 1970. Relationships of nutritional and environmental factos to selected rooted aquatic macrophytes. Part 1. Factors affecting growth of Najas in Pickwick reservoir. National fertilizer Center, T.V.A., Mussel Shoals, Alabama.

Moss, B. 1976. The effects of fertilization on community structure and biomass of aquatic macrophytes and epiphytic algal populations: an ecosystem experiment. J. Ecol. 59: 154-160.

Moyle, J.B. 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. Am. Midl. Nat. 34: 402-420.

Nichols, S.A. 1982. Sampling characteristics of macrophyte biomass. Wat. Res. Bull. 18: 521-523.

Ozimek, T., and A. Kowalczewski. 1984. Long term changes in the submerged macrophytes in eutrophic Lake Mikolajskie (North Poland). Aquat. Bot. 19: 1-11.

Pip, E. 1979. Survey of the ecology of submerged aquatic macrophytes in central Canada. Aquat. Bot. 7: 339-357.

Pokorny, J., J. Kvet, J.P. Ondok, Z. Toul, and I. Ostry. 1984. Production-ecological analysis of a plant community dominated by Elodea canadensis Michx. Aquat. Bot. 19: 263-292.

Prepas, E.E. 1983. Total dissolved solids as a predictor of lake biomass and productivity. Can. J. Fish. Aquat. Sci. 40: 92-95.

Provencher, M., B. Belanger, and H. Durocher. 1979. Caracterisation de la qualite de l'eaux de la riviere Yamaska Nord: Rapport complementaire. Service de la Qualite des Eaux, Minitere des Richeses Naturelles, Quebec.

_______ . 1973. Inventaire physico-chimique de 147 lacs du Quebec. Ministerie des Richeses naturalles. Quebec. 171 pp.

Rawson. D.S. 1955. Morphometry as a dominant factor in the productivity of large lakes. Verh. Internat. Verein. Limnol. 12: 164-175.

Rodhe, W. 1949. The ionic composition of lake waters. Verh. Intern. Verein. Limnol. 10: 377-386.

Ryder, R.A. 1965. A method to estimate the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214-218.

Sakamoto, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. Arch. Hydrobiol. 62: 1-28.

Sartory, D.P., and J.V. Grobbelaar. 1984. Extractions of chlorophyll-a from freshwater phytoplankton for spectrophotometric analysis. Hydrobiologia 114: 177-187.

Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes. Science 195 :260-262.

Seddon, B. 1972. Aquatic macrophytes as limnological indicators. Freshwater Biol. 2: 107-130.

Service de la qualite des eaux. 1978. Etude limnologique: Lac D'Argent, Lac Montjoie, Lac Brompton, Lac Bowker, Lac Roxton, Lac Brome, Lac Stukely, Lac Magog, Lac Waterloo, Lac Massawippi, Lac Orford, et Lac Lovering. Ministere des Richeses Naturelles. Quebec.

Small, J.W., Jr., D.I. Richard, and J.A. Osborne. 1985. The effects of aquatic vegetation removal by grass carp and herbicides on the water chemistry of four Florida lakes. Freshwater Biol. 15: 587-596.

Smith, C.S., and M.S. Adams. 1986. Phosphorus transfer from sediments by Myriophyllum spicatum. Limnol. Oceanogr. 31: 1312-1321.

Sondergaard, M., and K. Sand-Jensen. 1979. carbon uptake by leaves and roots of Litorella uniflora (L.) Aschers. Aquat. Bot. 6: 1-12.

Spence, D.H.N. 1967. Factors controlling the distribution of freshwater macrophytes, with particular reference to the Scottish lochs. J. Ecol. 55: 147-170.

______ . 1981. The zonation of plants in freshwater lakes. Adv. Ecol. Res. 12: 37-125.

______, and S.C. Maberly. 1985. Occurrence and ecological importance of HCO_3 use among aquatic higher plants. p.p. 125-143. In W.J. Lucas and J.A. Berry (eds.). Inorganic carbon uptake by aquatic phtotosynthetic organisms. The American Society of Plant Physiologists, Baltimore, USA.

Straskraba, M. 1980. The effect of physical variables on freshwater production: an analysis based on models. p.p. 13-84. In E.D. Le Cren and R.H. Lowell-McConnell (eds.). The functioning of freshwater ecosystems. Cambridge Univ. Press. Cambridge.

Talling, J.F. 1976. The depletion of carbon dioxide from lake water by phytoplankton. J. Ecol. 64: 79-121.

Twilley, R.R., W.M. Kemp, K.W. Staver, J.C. Stevenson, and W.R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. I. Algal growth and effects on production of plants and associated communities. Mar. Ecol. Prog. Ser. 23: 179-191.

Waisel, Y., M. Agami, and Z. Shapira. Uptake and transport of ^{86}RB, ^{32}P, ^{36}Cl and ^{22}Na by four submerged hydrophytes. Aquat. Bot. 13: 179-186.

Walker, T.A. 1982. Use of a Secchi disc to measure attenuation of light for photosynthesis. J. Appl. Ecol. 19:539-544.

Wetzel, R.G., and J. B. Grace. 1983. Aquatic plant communities. p.p. 223-290. In: E.R. Lemond (ed.), CO_2 and plants. AAAS selected symposiums series. Westview Press, Boulder.

Whitfield, A.K. 1984. The effects of prolonged aquatic macrophyte senescence on the biology of the dominant fish species in a Southern African coastal lake. Est. Coastal Shelf Sci. 18: 315-329.

Wium-Anderson, S. 1971. Photosynthetic uptake of free CO_2 by the roots of *Lobelia dortmanna*. Physiol. Pl. 25: 245-248.

CHAPTER IV

The influence of lake morphometry on the response of submerged macrophytes to sediment fertilization

ABSTRACT

The influence of lake morphometry on the growth of submerged macrophytes in response to nutrient fertilization of sediments at sites of varying bottom slope (steep/gentle), and wave exposure (high/low), and depth (1.0 and 2.5 m) was studied in Lake Memphremagog (Quebec-Vermont).

On average the biomass increases were 2.1 times greater for fertilized macrophytes than for the paired controls. The extent of this growth response was greater in the 1.0 m sites, where growth directly related to control biomass. At the 2.5 m sites the response was lower, and it decreased as exposure to waves and bottom slope increased. The lower response at 2.5 m (depth of maximum biomass) indicates that factors other than nutrient levels (such as light levels or littoral slope) limit submerged biomass here. This is particularly so in sites with relatively high biomass. Overwintering plants showed greater response to fertilization than those growing from seeds or roots.

Overall, the extent of the response of submerged macrophyte growth to nutrients depends on the energy environment (i.e. depth, wave exposure and slope) of the littoral. The influence of these physical factors explains the lack of success in obtaining strong correlations between nutrient levels and macrophyte growth.

INTRODUCTION

The importance of the primary productivity of submerged macrophytes varies greatly among lakes (Wetzel and Hough 1973). Because the biomass of submerged plants is frequently lower in oligotrophic than in eutrophic lakes and because summer phytoplankton biomass correlates well with water nutrient levels, there is a widespread belief that macrophyte biomass should be a function of nutrient availability. However, the lower biomass of submerged macrophytes in most oligotrophic lakes is primarily a function of lake morphometry, rather than of nutrient concentrations (Duarte et al. 1986), and reflects the greater depth of oligotrophc lakes (Rawson 1955, Sakamoto 1966). Increased nutrient levels may, in fact, reduce macrophyte biomass by increasing algal biomass and so reducing underwater irradiance (Moss 1976, Mulligan et al. 1976, Twilley et al. 1985).

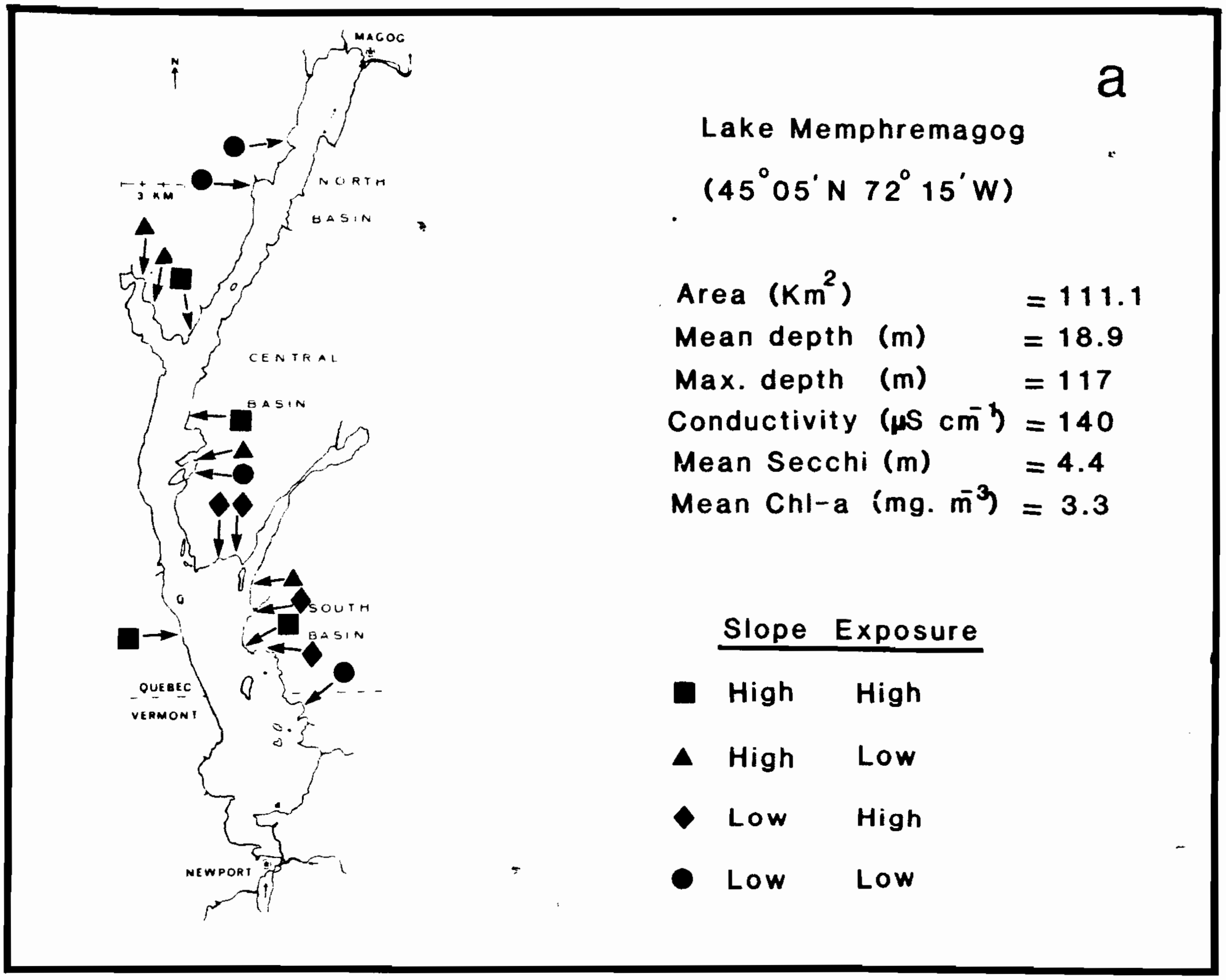
Rooted submerged macrophytes derive most of their nutrient supply from the sediments (Carignan and Kalff 1980, Nichols and Keeney 1976, Mantai and Newton 1982, Bristow 1975). However, attempts to demonstrate a relationship between submerged biomass and sediment nutrient levels have been inconclusive (see Anderson 1976, Langeland 1982), and sediment enrichment experiments in a Canadian lake yielded only modest increases in biomass (Anderson and Kalff 1986), although more substantial increases in biomass following sediment fertilization have been shown in an estuary (Orth 1977). Increasingly, the literature points to the importance of wave action (Jupp and Spence 1977) and littoral slope (Duarte and Kalff 1986) in determining submerged macrophyte biomass.

The objective of this study is to resolve the paradox that submerged macrophytes appear not to be nutrient limited in oligotrophic and mesotrophic lakes, even though phytoplankton are. At least two explanations are possible: (1) that submerged macrophytes in oligotrophic or mesotrophic lakes are not nutrient limited because they can satisfy their nutrient demand from the sediments or (2) that the strong influence of the energy environment (such as wave action and littoral slope) on submerged macrophytes mask their nutrient deficency. To resolve this, we selected sites of different energy environment (i.e. differing in exposure to waves, littoral slope and depth) in Lake Memphremagog (Quebec-Vermont) and fertilized the sediments there to quantify the growth response of the natural plant assemblages.

MATERIALS AND METHODS

The experiment was conducted in Lake Memphremagog (Québec-Vermont), a large oligotrophic to mesotrophic lake which is sufficiently diverse morphometrically to provide a wide range of wave exposures and littoral slopes (Fig. 1). We tested the effect of the energy environment on the response of submerged plants to fertilization in sites exposed and protected from wave action, with steep and gentle slopes, and by using experimental plots at 1.0 and 2.5 m so as to consider the decrease in energy with increasing depth. The two depths were selected to represent the upper rooting depth in the lake (0.9 m) where wave action is most severe, and the depth of maximum submerged biomass (2.6 m), which is partially a function of light levels (Chambers and Kalff 1985a). To account for the normal 0.5 m decrease in water level over the summer the plots were initially established 0.5 m deeper than the depths here reported. Four experimental quadrats were matched with 4 controls at each of the two depths at sixteen sites (Fig. 1), representing four replicated habitats for each combination of slope and exposure (high or low), yielding a total of 256 plots. At each site, the littoral slope (%) was measured with an echosounder (Sitex- Honda, model HE-356b) and the wave exposure calculated in two ways: 1) following a modified weighted effective fetch method (see Duarte and Kalff 1986) with the wind frequency and speed obtained from a lakeside meteorological station (Petticrew, unpubl. data), and 2) as the area of water exposed to each site, or effective area (Earea, Km^2), measured from a 1:34,130 map with a digitizer (Hi-Pad, Houston Instruments). The second method was used to account for the fact that the wave direction in Lake Memphremagog may form angles as high as 60^{o} with the direction of the wind, and wind measurements may not be representative if

Figure 4.1 Map of Lake Memphremagog showing the sites of the 4 different treatments and the main morphometric and water characteristics of the lake.



not taken at each site. The water transparency at the 16 sites was measured three times during the course of the experiment using a 20 cm Secchi disk.

Unlike previous in situ nutrient manipulations (Anderson and Kalff 1986, Chambers and Kalff 1985b), we used the natural plant community and sediments to prevent possibly confounding factors like transplant stress, differential success in rooting depending on the substrate, or competition with the natural plants. Furthermore, results obtained from transplants of a single species may not be extrapolatable to natural communities adapted to the particular conditions in each plot. However, the variability in the natural community structure, both in terms of initial biomass and species composition, guarantees a larger unexplained variance than if manipulated plots had been used. We attempted to minimize this source of variance by using paired plots to account for some of the patchiness within sites. The four fertilized plots at each depth were placed 9 m apart, and the control plots at 3 m from the corresponding fertilized one. The individual plots were marked with styrofoam floats 0.5 m above the sediments. SCUBA divers fertilized the experimental sites between June 6 and 9 with a 15 cm long spike of slow release fertilizer with 200 grams of fertilizer containing nitrogen, phosphorus and potasium in the ratio 3 N: 1 P: 1 K. At this time the plants were either still dormant or just starting to emerge (surface water temperature 14^{o}C). When possible, the fertilizer spikes were pushed to a depth of 15 cm in the sediments, thereby encompassing the depth of the highest root density in Lake Memphremagog. A second spike was placed within 10 cm of the first on 15 or 16 of July so as to guarantee abundant nutrients. Nutrient supply to the plants in the plot was not considered to be a problem because, although diffusion coefficients in sediments are low, the long vascular root systems of the species involved (ranging from 7-10 cm. in diameter for Najas flexilix to almost 1 m in Myriophyllum spicatum) have been shown to be very efficient in long range (20-30 cm.) nutrient transport (Bottomley and Bayly 1984, Mantai and Newton 1982). Furthermore, Orth (1977), who used a very similar fertilization technique to ours, reported that responses to fertilization were visually evident at distances well beyond the 0.25 m^2 area covered by our plots.

Using SCUBA, we harvested the experimental sites between 7 and 11 August, about 10 days before peak biomass to minimize natural plant mortality. All the aboveground parts of the submerged plants rooted inside a 0.25 m^2 quadrat, centered on the location where the first spike had been inserted, were collected and then refrigerated until processed. The plants were rinsed free of detritus and animals; those species that do not overwinter above ground, here refered to as annuals (mostly Vallisneria americana, Najas flexilis and Heteranthera dubia), were separated from "overwintering plants" (largely Myriophyllum spicatum, Potamogeton praelongus, and Potamogeton robinsii) and both classes weighed to the nearest 0.01 g, after excess water had been removed with a lettuce spinner.

Just prior to harvesting a sediment core was taken with a plexiglass corer (5 cm internal diameter) to a depth of 10 cm, to obtain a measure of water content, organic content and total phosphorus of the sediment, and the sediment depth was measured in 4 random locations at each quadrat using a metal rod. Sediment water content was measured to represent the sediment conditions since it is closely related to the sediment granulometry, bulk density, nutrient levels, redox potential, and even metal levels (Hakanson 1977, Hakanson 1981, Duarte and Kalff 1986). The sediment was extruded into a container and frozen within 3 h of collection for subsequent analysis. At that time, the sediments were first mixed, the water content determined after drying overnight at 110 ^{o}C, followed by the computation of organic content from the mass loss after overnight ignition at 540^{o} C. Analysis of total phosphorus followed Andersen (1976).

Due to the dissapearance of 24 markers only 241 of the 256 plots were recovered at the end of the experiment. Because of the nature of the experiment the slope and fetch could not be exactly duplicated at the 4 replicate sites (Table 1). The paired controls permitted some correction for local differences in the weedbed biomass and sediment characteristics among the four replicate plots in each treatment. We used an analysis of covariance to further remove the effects of uncontrolled variables and to account for variations in the control variables within treatments (Steel & Torrie 1960).

RESULTS AND DISCUSSION

Characteristics of control plots.

The mean slope, exposure and sediment depth values for the different treatments are presented in Table 1. The marked differences in sediment characteristics at the two depths reflect the greater effect of wave action in shallower waters. Sediment layers at 1 m were thinner and coarser, with lower water content and lower phosphorus concentration than those at 2.5 m, and had lower organic contents, with their associated lower nitrogen levels (Brady 1974) than those at 2.5 m (Table 1). No plants were found in 12 of the 128 control plots at the start of the experiment, however only 7 of these, all shallow exposed quadrats, were bare of vegetation by the end of the experiment. The biomass in the control plots ranged therefore from 0 to 1745 g fresh wt. m^{-2} at a deep and gently sloped site (Table 1). The biomass of controls was higher in the 2.5 m than in the shallow plots (t test, $P< 0.0001$), and, at the greater depth, it was higher on the gently sloped sites (t test, $P<0.0001$). Overwintering plants (i.e. Myriophyllum spicatum, Potamogeton praelongus and Potamogeton robinsii), dominated the biomass in the deep stands, whereas annuals (largely Vallisneria americana, Najas flexilis, Potamogeton gramineous) were dominant in the shallow plots (Fig. 2, Wilcoxon rank signed test, $P <0.001$). Water transparency decreased slightly from south to north ($r = 0.34$), the average Secchi transparencies for the 16 sites ranging from 3.9 to 5.1 m.

Influence of nutrient additions on biomass.

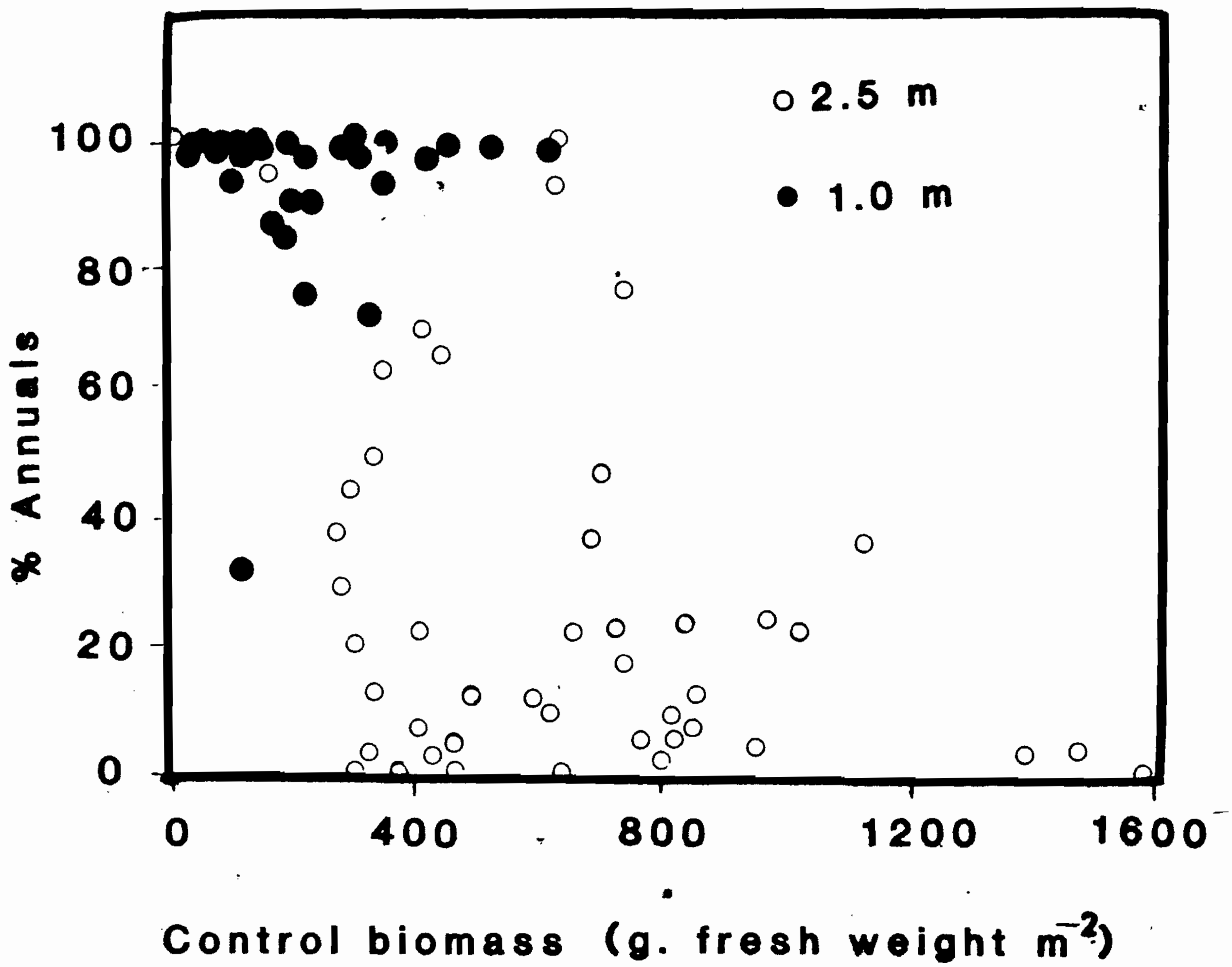
The biomass in the fertilized plots was, on average, more than two fold greater than that in the paired controls (Wilcoxon rank signed

Table 4.1 Environmental characteristics of the experimental sites and sediment covariates, showing the differences between treatments (high and low, H and L) treatments and the shallow and deep treatments (1.0 m and 2.5 m). All variables differ significantly at the two levels ($P < 0.05$).

Variable	Level	Mean	S.E.
Earea (km^2)	H	15.9	1.5
	L	3.0	0.6
Slope (%)	H	7.5	0.4
	L	2.0	0.08
T.P. (mg. / g. dry wt.)	1.0 m	0.52	0.04
	2.5 m	0.87	0.04
W. C. (% fresh wt.)	1.0 m	32.4	0.91
	2.5 m	47.3	1.37
O. M. (% dry wt)	1.0 m	2.53	0.24
	2.5 m	10.33	0.74
Sed. Depth (cm.)	1.0 m	21	12
	2.5 m	132	33
Secchi disk (m)	All	4.5	0.4

Earea = effective area; W. C. = sediment water content; T.P. = sediment total phosphorus; O.M. = sediment organic matter.

Figure 4.2 The proportional contribution of annual plants to the control biomass as a function of the control biomass for shallow and deep plots.



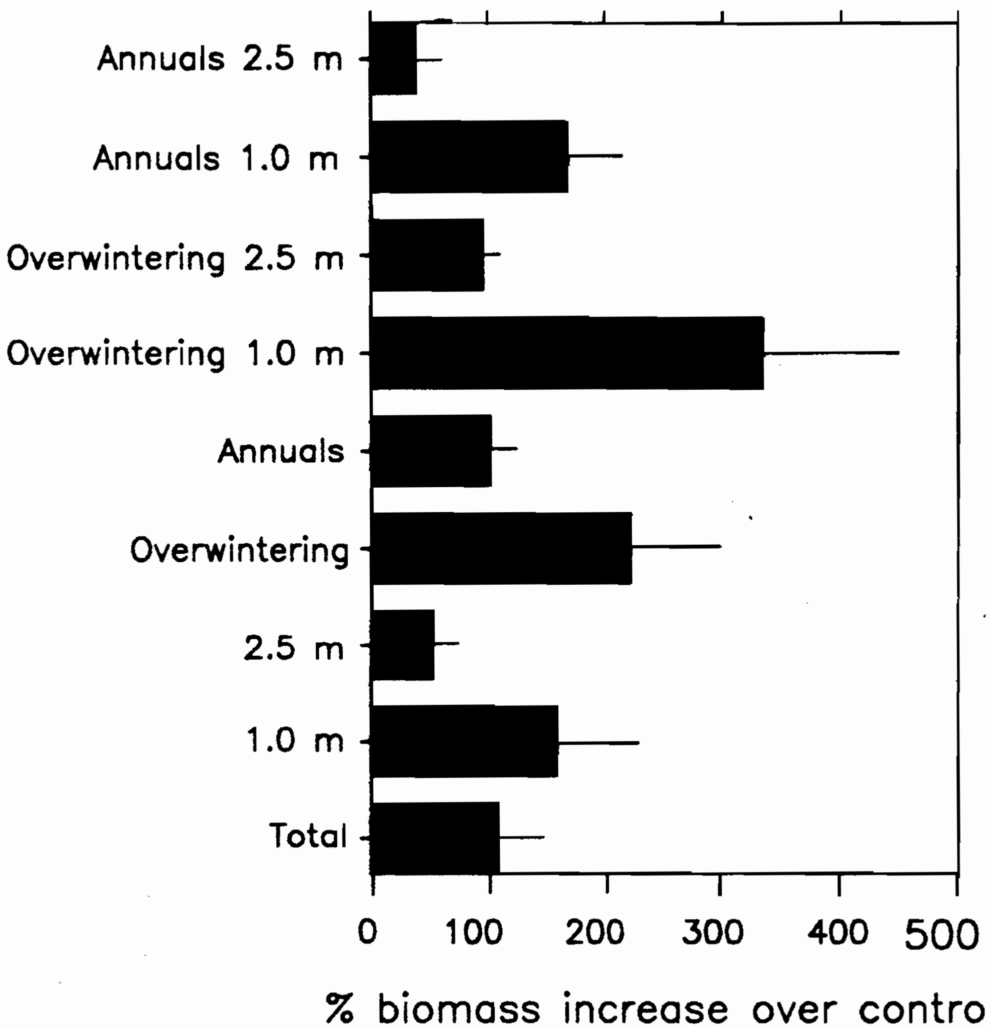
test; P < 0.0001; Fig. 3). This growth response is greater than reported for previous in situ fertilization experiments in this lake (Anderson and Kalff 1986). The strong responses obtained may be attributed to (1) the use of natural communities, preventing transplant stress and space problems due to confinement and (2) the use of large amounts of slow-release fertilizer.

Overwintering plants responded more strongly to nutrient addition than annual plants (Wilcoxon rank signed test, P<0.0001; Fig. 3), indicating that established vegetation used the added nutrients more readily than did the annuals. The greater response of overwintering plants (Fig. 3), suggests that transplant experiments may underestimate the effect of fertilization because they force all plants to behave like annuals (see Chambers and Kalff 1985b, Anderson and Kalff 1986). At deeper sites, the annual plants did not respond significantly to fertilization, whereas overwintering plants responded in both shallow and deep plots, their increase being greater in the shallow sites (Fig 3).

Morphometric influences on biomass response to fertilization.

There was a significant response to fertilization at all sites (t-test, P<0.001) except the 2.5 m habitats with low fetch and steep slope (t-test, P>0.05). Because the response to fetilization varied considerably among sites (Fig. 3) we tested whether this variability could be partially attributed to differences in littoral slope and exposure to waves. We examined the influence of these morphometric factors on the growth response using regression analysis where the wave exposure of each site was measured as the effective area (Earea, Km^2), which is better related to sediment texture, as reflected in the water content (r = 0.62), than is the weighted effective fetch (r = 0.53), and the experimental depth was

Figure 4.3 The average percent biomass increase in the fertilized plots over the paired controls: (experimental biomass - control biomass) / control biomass , for all plots, the two experimental depths separated, for overwintering and annual plants and for the response of overwintering and annual plants at the two depths. The bars represent ∓ 1 standard error.



represented as a categorical variable taking the values 1 (2.5 m) and 0 (1.0 m). The analysis of covariance of the increase in growth (experimental biomass - control biomass, g. fresh wt 0.25 m^{-2}) showed that increasing exposure to wave action and slope significantly reduced the fertilization response:

$$\text{Growth increase} = 961 - 4.8\ (14.4)\ \text{Earea} - 711\ (7.2)\ \text{slope} + 61.2\ (5.3)\ \text{slope} * \text{Earea} \qquad (1)$$

$$r^2=0.28;\ \text{E.M.S.} = 3137.3;\ N = 105$$

where the partial F-values are shown in brackets. All non significant ($P>0.05$) treatment variables (i.e. depth), covariates (control biomass, sediment water content, sediment organic content, sediment phosphorus content, sediment depth, and water transparency), and interaction terms are not shown. Evidently, plants in more exposed and steep sites were unable to use the added nutrients to the same extent as those in protected zones. Thus, plants in protected and gently sloped sites are more sensitive to nutrient changes, whereas the stress exerted on plants in steep or exposed environments limits their capacity to respond to nutrient additions.

Wave exposure may affect plants directly by the physical stress of waves or indirectly by increasing sediment coarseness and preventing extensive root development. This indirect effect appears unlikely, since differences in sediment characterisitics, such as water content, organic content or total phosphorus did not covary with the increase in biomass.

Depth dependent influences of morphometric factors on plant response to fertilization.

Since the wave action is, for a given exposure, more severe in the 1.0 m than in the 2.5 m depth, the nature of its influence on the response to fertilization may differ at the two depths. Besides, the overall influence of initial (control) biomass on fertilization responses was opposite in the two depths (Fig. 4), and this difference tends to confound the previous analysis. Consequently, the growth responses of deep and shallow stands were analyzed separately.

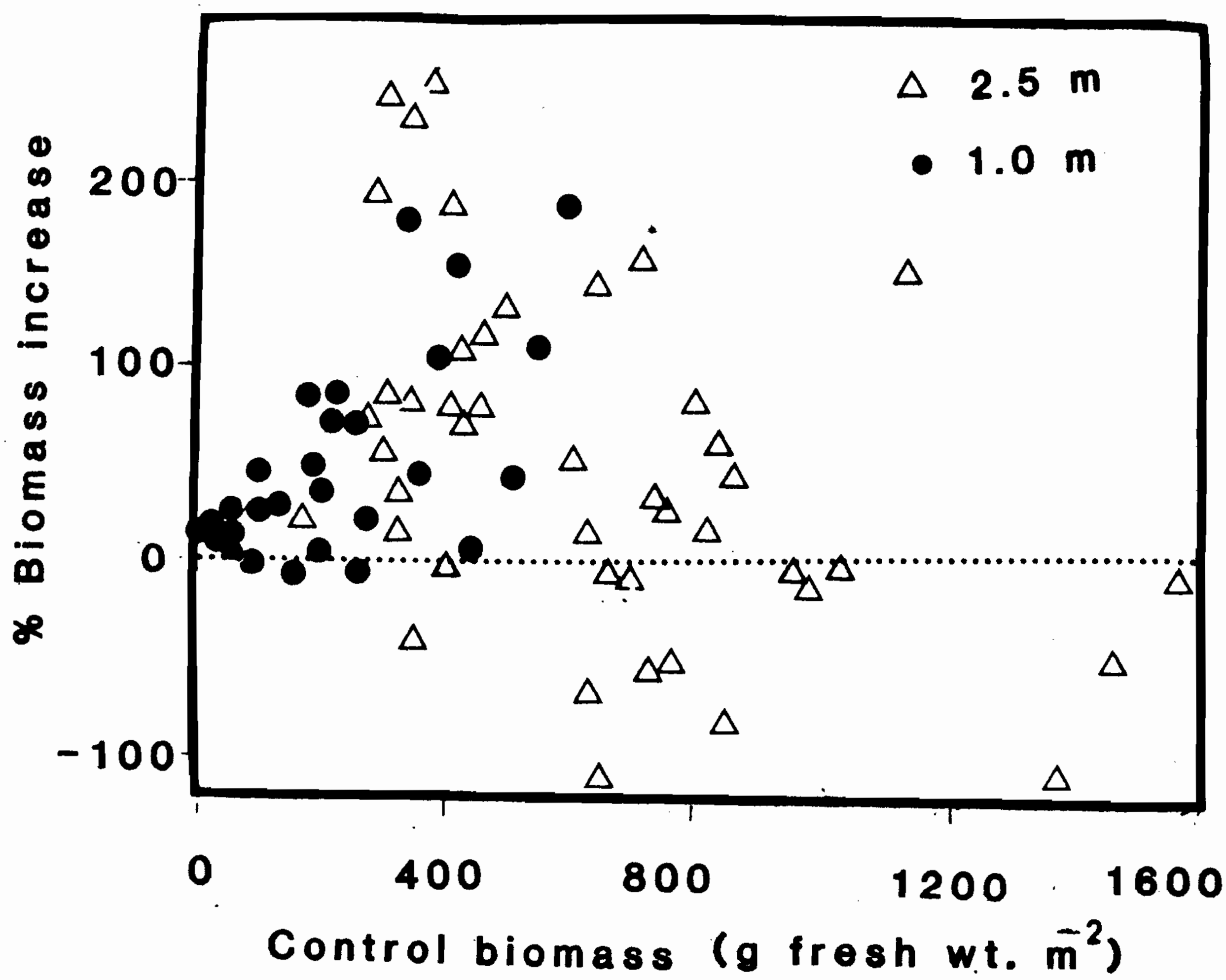
The analysis for the 2.5 m depth explained 32% of the variation in growth increase and showed that the response decreased with increasing exposure and with increasing control biomass:

Growth increase = 214 - 7.7 (10.4) Earea - 0.35 (7.4) control biomass (2)

$r^2 = 0.32$, E.M.S. = 5488; N =49

The reduced response to fertilization at sites of high control biomass (Fig. 4) suggests that the biomass of deep macrophytes may be light limited. Despite the fact that the experimental depth (2.5 m) was well above the depth of maximum colonization for the lakes (6.2 m), the reduction in the response with increasing biomass suggests that as biomass increases self-shading results in light limitation. This may appear inconsistent with the lack of significant effect of the differences in water transparency among sites, however, these differences are very small (Table 1) and are probably negligible compared to the influence of the plants themselves on the light extinction. Canopy species (e.g. _Myriophyllum spicatum_, and _Potamogeton praelongus_), which extend their biomass throughout the water column, dominated in this depth. The specific extinction coefficients due to plant material for these species range around 0.0014 and 0.0011 m^2 g fresh wt.$^{-1}$ (Westlake 1964). Given the range of the control biomass (2 - 1600 g. fresh wt. m^{-2}) this results in specific extinction coefficients for the plants (K_b) ranging between 0.0011 - 0.704 m^{-1} (assuming that the plant biomass is homogeneously distributed

Figure 4.4 The relationship between the percent biomass increase over the control plots as a function of the control biomass for the 1.0 and the 2.5 m plots.



within the 2.5 m. water column) compared to extinction coefficients due to water and its associated particles (K_w) of 0.28 - 0.37 m^{-1} (assuming K_w= 1.47 / Secchi depth, Walker 1982). When these coefficients are combined to calculate the average light intensity within the 2.5 m deep water column (I_c, Riley 1956):

$$I_c = I_o \; (1 - 2.5 \; (K_w + K_b))/(2.5 \; (K_w + K_b) \qquad (3)$$

it is evident that plants not only contribute greatly to the extinction of the surface irradiance (I_o) within the water column (2.5 m), but also that the great variablility of their extinction coefficients compared to the narrow range of K_w dominates the variance in the light levels within the water column, rendering Secchi depth a poor descriptor of the light regime in the vegetated areas. Since the experimental depth of 2.5 m is relatively large compared to the wave height (between 0 and 0.5 m in Lake Memphremagog), the negative effect of exposure on the growth response (Eq. 2) may be due to a direct physical stress on the plant canopy, since plants here often extend close to the surface. Additionally, the increase in surface reflection of light with wave action, may have also decreased the light available for plant growth. Violent wind events may also create temporary turbid conditions, which could be missrepresented by our Secchi values due to the low sampling frequency (3 readings in 2 months). Despite the strong relationship between littoral slope and control biomass at 2.5 m (Duarte and Kalff 1986), the response to nutrient additions there is not dependent on the littoral slope (F test, $P>0.05$). This supports evidence presented (Duarte and Kalff 1986) that the relationship between slope and maximum submerged biomass is independent of nutrient levels.

The growth response in shallow sites was proportional to the control biomass (r^2= 0.50), and no effect of morphometric factors was noted:

$$\text{Growth increase} = 33.9 + 0.65\ (47.7)\ \text{control biomass} \qquad (4)$$

$$r^2 = 0.50;\ \text{E.M.S. } 917.3;\ N = 56$$

this indicates that, in contrast to the plants at 2.5 m, where response to nutrient additions was largely a function of the energy environment, nutrient limitation per se controls submerged growth at 1.0 m. Coarser sediments, lower levels of total phosphorus and organic matter in the sediment (Table 1), and higher light in the shallower sites accentuate the importance of nutrient limitation for growth. The marked response of shallow water plants to nutrient additions (Fig. 3) indicates the importance of erosion of fine materials by the combined effects of slope and wave action (Hakanson 1977), which reduce effective nutrient levels in these areas. Here, nutrient deficiency becomes more important to the plants than the direct physical stress resulting from exposure to waves and currents. Additionally, ice scouring in the spring may also be responsible for sediment erosion. Further, the absence of a direct relationship between plant response to fertilization at 1.0 m and exposure to waves suggests that ice scouring in the spring, which is relatively homogeneous around the lake shore, may have a greater influence on sediment erosion than wave action. Although the amount of nutrients supplied was similar in all sites, their dynamics may well have differed depending on the wave intensity, sediment grain size, and slope of the different locations. This lack of precise control on the treatment variables may be partially responsible for the error remaining in the analysis.

In summary, nutrient limitation of submerged macrophytes growth in this lake can be demonstrated at the two depths studied. However, the extent of this limitation differs between shallow and deep sites and varies with the degree of physical stability of the littoral zone. In contrast to the idea that direct physical disturbance by wave action controls macrophyte biomass in lacustrine littoral regions (Jupp and Spence 1977, Spence 1982), these results implicate nutrient limitation as the proximal regulating factor. It appears that wave action at the shallow sites results in the erosion of fine grain particles and associated nutrients, enhancing nutrient limitation of growth in these sites. On the other hand, the direct physical stress produced by wave action, together with the degree of slope and light levels appear to contribute to growth regulation at the depth of maximum biomass (2.5 m).

The field sites in this study represent wide ranges of wave exposure, littoral slope and sediment characterisitics. Thus the results presented here should be applicable to other oligotrophic or mesotrophic lakes. A model developed from similar field data in Lake Memphremagog and predicting the maximum biomass of submerged plants as a function of littoral slope was found applicable to other temperate lakes (Duarte and Kalff 1986). Extrapollation from our experiment suggests that the macrophytes of large lakes with high wave action and steep slopes should respond less to sediment nutrient enrichment at the depth of maximum biomass than those in smaller lakes or well protected bays with similar light levels, whereas the response in shallower zones would not be influenced by lake size. The effect of lake water enrichment through cultural eutrophication will differ from that of sediment enrichment. All the available evidence indicates that submerged biomass will be severely reduced by the decreased light penetration associated to the higher algal biomass characteristic of lake water enrichment (Moss 1976, Mulligan et al. 1976, Twilley et al. 1985, Duarte et al. 1986).

The lake littoral is a zone of great complexity, where physical and chemical factors interact to produce very different responses to the same disturbance. This experiment shows that submerged macrophytes can be nutrient limited in oligotrophic or mesotrophic lakes, and suggests that lack of success in obtaining significant correlations between nutrient levels and macrophyte growth may be due to the modulation of this link by physical factors like slope, wave action and light.

REFERENCES

Andersen, J.M. 1976. An ignition method for determination of total phosphorus in lake sediments. Water Res. 10: 329-331.

Anderson, M. G. 1978. Distribution and production of sago pondweed (Potamogeton pectinatus L.) on a northern prairie marsh. Ecol. 59: 154-160.

Anderson, R.M., and J. Kalff. 1986. Nutrient limitation of Myriophyllum spicatum growth in situ. Freshwat. Ecol. In press.

Bottomley, E.Z., and I.L. Bayly. 1984. A sediment porewater sampler used in the root zone studies of the submerged macrophyte, Myriophyllum spicatum. Limnol. Oceanogr. 29: 671-673.

Brady, N.C. 1974. The nature and properties of soils. 8th Ed. MacMillan.

Bristow, J.M. 1975. The structure and function of roots in aquatic vascular plants. p.p. 221-236. In: J.G. Torrey and D.T. Clarkson (eds.), The development and function of roots. Academic.

Carignan, R., and J. Kalff. 1980. Phosphorus sources for aquatic weeds: water or sediments. Science 207: 987-989.

Carlson, R.E. 1977. A trophic state index for lakes. Limnol. Oceanogr. 22: 361-369.

Chambers, P.A., and J. Kalff. 1985a. Depth distribution and biomass of submerged macrophyte communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42: 701-709.

________, and J. Kalff. 1985b. The influence of sediment composition and irradiance on the growth and morphology of Myriophyllum spicatum L. Aquat. Bot. 22: 253-263.

Duarte, C.M., and J. Kalff. 1986. Littoral slope as a predictor of the maximum biomass of submerged macrophyte communities. Limnol.

Oceanogr. 31: 1072-1081.

_______ , _______ , and R. H. Peters. 1986. Patterns in biomass and cover of submerged macrophytes in lakes. Can. J. Fish. Aquat. Sci. 43: 1900-1908.

Hakanson, L. 1977. The influence of wind, fetch and water depth on the distribution of sediments in lake Vanern, Sweden. Can. J. Earth Sci. 14: 397-412.

Hakanson, L. 1981. On lake bottom dynamics: the energy-topography factor. Can. J. Earth Sci. 18: 899-909.

Jupp, B.P., and D.H.N. Spence. 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. II. Wave action, sediments, and waterfowl grazing. J. Ecol. 65: 431-446.

Langeland, K. A. 1982. Relationships among hydrosoil, water chemistry, transparency, chlorophyll a, and submersed macrophyte biomass. Ph.D. dissertation, The University of Florida. 142 pp.

Mantai, K.E., and M.E. Newton. 1982. Root growth in Myriophyllum: a specific plant response to nutrient availability?. Aquatic Botany 13: 45-55.

Moss, B. 1976. The effects of fertilization and fish on community structure and biomass of aquatic macrophytes and epiphytic algal populations: an ecosystem experiment. J. Ecol. 64: 313-342.

Mulligan, H.F., A. Baranowski, and R. Johnson. 1976. Nitrogen and phosphorus fertilization of aquatic plants and algae in replicated ponds. I. Initial response to fertilization. Hydrobiologia 48: 109-116.

Nichols, D.S., and D.R. Keeney. 1976. Nitrogen nutrition of Myriophyllum spicatum: uptake and translocation of N by shoots and roots. Freshwater Biol. 6: 145-154.

Orth, R. J. 1977. Effect of nutrient enrichment on growth of the eelgrass Zoostera marina in the Chesapeake Bay, Virginia, USA. Mar. Biol. 44: 187-194

Peltier, W. H., and E. B. Welch. 1970. Factors affecting growth of rooted aquatic plants in a reservoir. Weed Sci. 18: 7-9.

Rawson, D.S. 1955. Morphometry as a dominant factor in the productivity of large lakes. Verh. Internat. Ver. Limnol. 12: 164-175.

Riley, G.A. 1957. Phytoplankton of the North Central Sargasso Sea, 1950-52. Limnol. Oceanogr. 2: 252-270.

Sakamoto, M. 1966. Primary production by phytoplankton community in some japanese lakes and its dependence on lake depth. Arch. Hydrobiol. 62: 1-28.

Spence, D.H.N. 1982. The zonation of plants in freshwater lakes. Adv. Ecol. Res. 12: 37-125.

Steel, R.G.D., and J.H. Torrie. Principles and procedures of statistics. McGraw Hill.

Twilley, R.T., W.M. Kemp, K.W. Staver, J.C. Stevenson, and W. R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. Mar. Ecol. Prog. Ser. 23: 179-191.

Walker, T.A. 1982. Use of a Secchi disc to measure attenuation of underwater light for photosynthesis. J. Appl. Ecol. 19: 539-544.

Westlake, D. F. 1964. Light extinction, standing crop and photosynthesis within weed beds. Verh. Internat. Verein. Limnol. 15: 415-425.

Wetzel, R.G., and R.A. Hough. 1973. Productivity and role of aquatic macrophytes in lakes. An assessment. Pol. Arch. Hydrobiol. 20: 9-19.

CONCLUSION

The results in this thesis provide a new perspective on the ecology of the littoral zone, emphasizing its complexity in relation to the pelagic zone. This complexity is a consequence of greater habitat heterogeneity. Littoral organisms live attached to a substrate, and are therefore affected by the environmental gradients associated with depth. These gradients are normally disrupted in the pelagic zone by vertical mixing. Littoral complexity is manifested in the relationships between submerged macrophytes and environmental conditions.

Whereas the cover of submerged or emergent macrophytes can be estimated from the underwater light climate or from the climate and morphometry of the lake respectively (Chapter I), the relationship between macrophyte biomass and environmental conditions is more complex. The variability in submerged biomass within a lake is primarily a function of the littoral slope (Chapter II), while chemical properties of the water, in particular total alkalinity, assume greater importance when the mean biomasses of submerged macrophytes in different lakes are compared (Chapter III). Although correlations between submerged biomass and sediment nutrients are weak, nutrient limitation of submerged biomass can be demonstrated, at least in oligotrophic or mesotrophic lakes (Chapter 4).

The models produced in this thesis allow the prediction of the area covered and the biomass of aquatic macrophytes. However, the main contribution of this work is not its application to prediction, because the accuracy achieved is insufficient for most uses of the models in management, but rather the complete view of the importance of different factors to the determination of macrophyte abundance provided by the models. In this respect, the importance of littoral slope over sediment conditions remains unexplained, however, I suspect that the strength of the relationship between submerged biomass and littoral slope results from the role of littoral slope as a integrator of many influences. Littoral slope influences the stability of the sediment; it correlates with many sediment characteristics; it also influences the mobility of sediment particles in the littoral zone; it modulates the energy discharge of waves; and it may also be related to the patterns of groundwater flow. Consequently, it is unlikely that the study of the relationships between submerged biomass and these processes, considered in isolation, will be as powerful as the relationship to littoral slope, which effectively summarizes all these processes and their interactions.

The new perspective on the ecology of aquatic macrophytes steming from these results is a consequence of the extensive use of field data. Field data allow the identification of important factors (such as littoral slope), whose indirect but multilevel influence on macrophyte ecology would remain hidden in laboratory studies.

APPENDIX A. Raw data on macrophyte, sediment and site characteristics of the sites sampled in Lake Memphremagog in 1984 (Chapter 2). Wc is the sediment water content in %; Orgm is the percent organic matter in the dry sediments; T.P. is the sediment total phosphorus concentration in mg g dry wt^{-1}; Depth is the water depth of the sampling location in m; Bio is the maximum biomass of submerged macrophytes in g fresh wt. m^{-2}; Slope is the littoral slope in percent; and Fetch is the weighted effective fetch in m.

Wc	Bio	Slope	Fetch	Orgm	Depth	T.P.
65.50	678.97	3.80	4519.00	12.65	3.00	0.44
67.43	575.20	11.70	4221.00	10.65	5.00	0.73
35.15	697.05	3.50	6668.00	2.61	3.00	0.54
66.09	798.24	4.20	2609.00	8.97	3.00	0.54
44.04	415.85	1.50	3591.00	5.10	2.40	0.79
34.85	487.84	6.60	3830.00	2.30	2.30	0.36
30.96	1111.13	2.28	3835.00	2.39	3.20	0.86
75.80	2614.41	0.30	714.00	10.59	3.50	0.58
84.31	846.37	0.90	3147.00	14.57	1.75	2.12
47.25	401.64	16.40	187.00	5.69	5.10	0.79
60.83	596.52	3.00	2915.00	23.57	2.25	0.74
47.28	2.95	6.40	3032.00	6.41	3.00	2.02
44.97	1184.61	2.20	3275.00	5.01	2.61	0.48
48.64	511.15	3.80	1272.00	3.85	1.50	0.62
43.91	807.96	2.10	2684.00	4.75	2.50	0.26
34.64	523.55	4.00	5153.00	2.21	2.40	0.31
37.34	905.93	1.50	457.00	2.46	2.00	0.57
32.34	42.60	9.80	8003.00	1.00	2.50	0.40
26.04	345.72	2.30	9018.00	2.35	2.50	0.33
30.32	214.17	5.00	3546.00	1.24	2.50	0.35
31.84	422.60	1.70	5546.00	1.23	2.00	0.27
27.22	221.85	10.90	2858.00	1.74	3.00	0.47
37.85	588.94	13.30	2485.00	3.20	3.00	0.72
44.16	294.79	2.60	2386.00	5.17	2.00	0.38
40.85	269.40	8.70	2860.00	3.81	2.50	.
27.24	155.28	16.40	1063.00	2.16	2.00	1.19
23.24	13.42	19.30	1548.00	2.30	2.00	0.24
83.67	1981.16	1.80	1902.00	45.43	2.00	0.62
40.25	439.18	5.40	8533.00	1.99	2.80	0.55
45.98	1171.82	1.10	1352.00	2.99	2.50	1.10
89.71	489.11	4.90	932.00	27.30	3.00	.
64.48	489.95	2.80	1664.00	7.31	3.70	0.31
49.00	942.11	1.10	1926.00	1.55	2.00	0.30
51.54	2059.46	0.40	862.00	3.84	2.00	0.34
55.91	1069.68	1.80	2147.00	9.53	3.00	0.05
74.38	0.00	30.30	2300.00	15.40	3.00	.
18.67	0.00	18.20	4425.00	1.97	4.50	.
97.05	0.00	25.20	511.00	41.99	3.00	.
35.26	0.00	14.00	2108.00	2.84	3.50	.
27.76	0.00	19.40	6445.00	2.57	3.00	.
33.06	0.00	12.00	4435.00	2.60	3.50	.
64.48	0.00	13.30	9890.00	8.44	2.00	.
24.74	0.00	18.00	5887.00	1.37	2.75	.
25.99	0.00	29.70	4724.00	3.61	4.00	.

APPENDIX B. Raw data for the submerged biomass, and lake and site characteristics of the 25 lakes sampled in 1985 (Chapter 3). Slope is the littoral slope in m of vertical change per horizontal m; Fecth in the effective area in Km^2; Alk is the total alkalinity in mg $CaCO_3$ l^{-1}; Secchi is the Secchi disc depth in m; Depth is the sampling depth in m; and Bioc is the biomass of submerged macrophytes in g. fresh wt. m^{-2}.

Site	Slope	Earea	Fetch	S. depth	Wc	Org.	TP
136	0.056	1.92	5.71		48.13		
	0.056	1.92	5.71		48.13		
	0.056	1.92	5.71		48.13		
	0.056	1.92	5.71		48.13		
Cove I.	0.011	1.952	8.29		37.71	1.69	2.118
	0.011	1.952	8.29		32.19	1.63	0.706
	0.011	1.952	8.29		32.13	1.51	0.692
	0.011	1.952	8.29		30.7		
486	0.0084	5.09			46.42		
	0.0084	5.09			46.42		
	0.0084	5.09			46.42		
	0.0084	5.09			46.42		
Green P.	0.0264	7.44	2.78		33	2.3	0.6870
	0.0264	7.44	2.78		35.5	2.1	0.6847
	0.0264	7.44	2.78		32.1	2.1	0.6932
	0.0264	7.44	2.78		32.38		
133	0.086	1.16	1.97		32.24	2.51	0.74
	0.086	1.16	1.97		43.83	3.93	0.72
	0.086	1.16	1.97		37.72	2.96	0.69
	0.086	1.16	1.97		66.64		
406	0.082	1.99	3.05		47.54	6.86	0.72
	0.082	1.99	3.05		26.35	1.85	0.75
	0.082	1.99	3.05				
	0.082	1.99	3.05				
414	0.051	2.07	5				
	0.051	2.07	5				
	0.051	2.07	5				
	0.051	2.07	5				
218	0.088	2.62	10.02		27.94	1.56	0.096
	0.088	2.62	10.02		31.43	1.69	0.092
	0.088	2.62	10.02		28.22	1.49	0.132
	0.088	2.62	10.02		29.75		
176	0.016	18.18	23.31		28.92	1.19	0.25
	0.016	18.18	23.31		28.92	1	0.24
	0.016	18.18	23.31		28.92	1	0.26
	0.016	18.18	23.31		28.92		
168	0.0236	26.15	24.26		24.3	1.6	0.5802
	0.0236	26.15	24.26		24.6	4.4	0.6380
	0.0236	26.15	24.26		24.2	1.3	0.5573
	0.0236	26.15	24.26		22.72		
225	0.0113	11.54	14.75		27.15		
	0.0113	11.54	14.75		27.15		
	0.0113	11.54	14.75		27.15		
	0.0113	11.54	14.75		27.15		
245	0.015	17.48	24.04		26.93		
	0.015	17.48	24.04		26.93		
	0.015	17.48	24.04		26.93		
	0.015	17.48	24.04		26.93		
444	0.057	7.48	8.13		40.36	3.84	0.4689
	0.057	7.48	8.13		43.89	6.07	0.7963

	0.057	7.48	8.13		42.87	6.11	0.5631
	0.057	7.48	8.13		38.5		
95	0.118	12.29	14.04		19.12	1.83	0.5620
	0.118	12.29	14.04		25.41	2.52	0.4394
	0.118	12.29	14.04		17.67	1.86	0.2877
	0.118	12.29	14.04		20.4		
238	0.041	13.96	15.02		25.61		
	0.041	13.96	15.02		25.61		
	0.041	13.96	15.02		25.61		
	0.041	13.96	15.02		25.61		
281	0.078	20.58	3.25		21.37		
	0.078	20.58	3.25		21.37		
	0.078	20.58	3.25		21.37		
	0.078	20.58	3.25		21.37		
136	0.056	1.92	5.71	105	69.69	18.33	1.06
	0.056	1.92	5.71	105	71.41	17.94	1.09
	0.056	1.92	5.71	105	65.82	17.37	1.07
	0.056	1.92	5.71	105	75.36		
Cove I.	0.011	1.952	8.29	87	49.06	3.79	0.676
	0.011	1.952	8.29	87	44.81	3.55	0.681
	0.011	1.952	8.29	87	49.16	3.62	0.663
	0.011	1.952	8.29	87	69.14		
486	0.0084	5.09			40.81		
	0.0084	5.09			40.81		
	0.0084	5.09			40.81		
	0.0084	5.09			40.81		
Green P.	0.0264	7.44	2.78	1.9	73	15	1.1609
	0.0264	7.44	2.78	1.9	60.7	10.8	1.0863
	0.0264	7.44	2.78	1.9	59.7	9	1.0863
	0.0264	7.44	2.78	1.9	54.3	8.8	1.1808
133	0.086	1.16	1.97	1.9	72.46	23.85	0.84
	0.086	1.16	1.97	1.9	64.21	11.06	0.92
	0.086	1.16	1.97	1.9	70.23	11.25	0.86
	0.086	1.16	1.97	1.9	49.12	6.14	0.85
406	0.086	1.99	3.05	45.2			
	0.086	1.99	3.05	45.2			
	0.086	1.99	3.05	45.2			
	0.086	1.99	3.05	45.2			
414	0.051	2.07	5	1.75	65.6	14.5	1.5332
	0.051	2.07	5	1.75	63.2	14.9	1.5314
	0.051	2.07	5	1.75			
	0.051	2.07	5	1.75			
218	0.088	2.62	10.02	153.7	40.88		
	0.088	2.62	10.02	153.7	40.88		
	0.088	2.62	10.02	153.7	40.88		
	0.088	2.62	10.02	153.7	40.88		
176	0.016	18.18	23.31	2	57.02	8.39	
	0.016	18.18	23.31	2	57.02	8.46	
	0.016	18.18	23.31	2	57.02	10.22	
	0.016	18.18	23.31	2	57.02		
168	0.0236	26.15	24.26	37.5	37.49		
	0.0236	26.15	24.26	37.5	37.49		
	0.0236	26.15	24.26	37.5	37.49		
	0.0236	26.15	24.26	37.5	37.49		
225	0.0113	11.54	14.75		26.8		
	0.0113	11.54	14.75		26.8		

	0.0113	11.54	14.75		26.8		
	0.0113	11.54	14.75		26.8		
245	0.015	17.48	24.04	66.76	32.77		
	0.015	17.48	24.04	66.76	32.77		
	0.015	17.48	24.04	66.76	32.77		
	0.015	17.48	24.04	66.76	32.77		
444	0.057	7.48	8.13	118.5	65.59	17.78	0.8697
	0.057	7.48	8.13	118.5	68.48	17.38	0.4738
	0.057	7.48	8.13	118.5	66.7		
	0.057	7.48	8.13	118.5	66.7		
95	0.118	12.29	14.04	1.22	51.56	6	0.9013
	0.118	12.29	14.04	1.22	58.3	6.44	0.9336
	0.118	12.29	14.04	1.22	42.93	7.45	0.8054
	0.118	12.29	14.04	1.22	46.71		
238	0.041	13.96	15.02	96.2	31.4		
	0.041	13.96	15.02	96.2	31.4		
	0.041	13.96	15.02	96.2	31.4		
	0.041	13.96	15.02	96.2	31.4		
281	0.078	20.58	3.25	6.2	29.7		
	0.078	20.58	3.25	6.2	29.7		
	0.078	20.58	3.25	6.2	29.7		
	0.078	20.58	3.25	6.2	29.7		

Site	St	Ft	Depth	Plot	Biomass	Bioper	Bioann	Bioc	Biocp	Bioca
136	0	0	1	1	90.47	4.97	85.5	48.23	3.83	44.4
	0	0	1	2	55.08	9.67	45.41	27.11	0.51	31.67
	0	0	1	3	60.44	2.18	58.26	32.18	9.88	10.5
	0	0	1	4	30.25	0	30.25	20.38	3.27	23.84
Cove I.	0	0	1	1	137.5	0	137.5	91.39	0	91.39
	0	0	1	2	120.55	0	120.5	112.23	0	112.23
	0	0	1	3	264.01	56.87	207.14	87.13	3.83	83.3
	0	0	1	4	331.38	1.85	226.51	150.87	0	150.87
486	0	0	1	1						
	0	0	1	2						
	0	0	1	3						
	0	0	1	4						
Green P.	0	0	1	1	91.03	3.7	87.33	69.58	0	69.58
	0	0	1	2	64.61	0	64.61	35.41	0	35.41
	0	0	1	3	41.35	0	41.35	20.67	0.5	20.67
	0	0	1	4						
133	1	0	1	1	109.16	0	109.16	78.75	0	78.75
	1	0	1	2	58.6	24.19	34.41	51.97	0	51.97
	1	0	1	3	34.99	13.1	21.89	42.61	6.46	36.15
	1	0	1	4	75.82	0	75.82	29.67	0	29.67
406	1	0	1	1	0	0	0	1.66	0	1.66
	1	0	1	2	31.51	1.34	30.17	16.81	0	16.81
	1	0	1	3	17.95	0	17.95	6.63	1.32	5.31
	1	0	1	4	127.15	7.3	119.85	46.2	6.92	39.28
414	1	0	1	1	18.67	0	18.67	19.66	0.37	19.29
	1	0	1	2	40.5	0	40.5	15.37	0	15.37
	1	0	1	3	42.08	24.39	15.08	19.27	0	19.27
	1	0	1	4	39.47	21.84	34.04	0	0	0
218	1	0	1	1	171.98	0	171.98	130.38	0	130.38
	1	0	1	2	137.04	0	137.04	65.83	0	65.83
	1	0	1	3	104.57	0	104.57	78.2	0	78.2
	1	0	1	4						
176	0	1	1	1	1.15	0	1.15	0.76	0	0.76
	0	1	1	2	30.92	0	30.92	8.32	0	8.32
	0	1	1	3	14.56	0	14.56	23.82	0	23.82
	0	1	1	4	97.54	0	97.54	47.98	0	47.98
168	0	1	1	1	0	0	0	3.1	0	3.1
	0	1	1	2	0	0	0	0	0	0
	0	1	1	3	16.49	0.27	16.22	0	0	0
	0	1	1	4	15.24	0	15.24	24.86	1.39	23.47
225	0	1	1	1	2.42	0	2.42	1.75	0	1.75
	0	1	1	2	3.4	0	3.4	1.47	1.2	0.27
	0	1	1	3	20	3.22	16.78	6.04	0	6.04
	0	1	1	4	24.8	0	24.8	3.1	0	3.1
245	0	1	1	1	1.73	0	1.73	0	0	0
	0	1	1	2	0	0	0	0	0	0
	0	1	1	3	0	0	0	0	0	0
	0	1	1	4	0	0	0	0	0	0
444	1	1	1	1	143.81	39	104.8	58.2	2.1	44.6
	1	1	1	2	257.21	74.15	183.06	107.45	0	107.45

	1	1	1	3	131.12	34.73	96.39	58.2	6	52.2
	1	1	1	4						
95	1	1	1	1	10.3	0	10.3	10.09	0	10.09
	1	1	1	2	16.47	0	16.47	14.04	0	14.04
	1	1	1	3	10.11	0	10.11	9.82	0	9.82
	1	1	1	4	6.26	0	6.26	8.53	0	8.53
238	1	1	1	1	57.46	2.15	55.31	66.52	0	66.52
	1	1	1	2	95.9	2.71	93.12	52.7	0.59	52.7
	1	1	1	3	45.7	0	45.7	26.76	0	26.76
	1	1	1	4	30.15	0	30.15	21.73	0	21.73
281	1	1	1	1	0	0	0	0	0	0
	1	1	1	2	0	0	0	0	0	0
	1	1	1	3	0	0	0	0	0	0
	1	1	1	4	8.41	0	8.41	10	0	10
136	0	0	2	1	171.85	146.35	25.5	154.99	57.38	18.13
	0	0	2	2	134.12	107.64	26.48	75.51	171.76	33.45
	0	0	2	3	224.86	219.06	5.8	205.1	139.47	15.52
	0	0	2	4	163.36	125.5	37.86	75.72	59.62	16.1
Cove I.	0	0	2	1	272.04	212.45	59.59	211.33	159.29	52.04
	0	0	2	2	255.65	212.9	42.75	123.84	107.74	16.1
	0	0	2	3	286.1	209.75	76.35	101.96	77.98	23.98
	0	0	2	4						
486	0	0	2	1						
	0	0	2	2						
	0	0	2	3						
	0	0	2	4						
Green P.	0	0	2	1	192.31	180.2	12.11	115.98	110	5.98
	0	0	2	2	204.94	202.41	2.53	151.66	132.58	19.08
	0	0	2	3	99.6	96	3.6	101.44	93.42	8.02
	0	0	2	4	177.9	170.05	7.85	107.17	103.92	3.25
133	1	0	2	1	214.36	150.41	63.95	185.48	153	32.48
	1	0	2	2	159.16	106.33	52.83	166.44	127.79	38.65
	1	0	2	3	161.54	130.79	30.75	172.07	107.48	64.59
	1	0	2	4						
406	1	0	2	1	324.76	274.88	49.88			
	1	0	2	2	139.31	124.03	15.28	190.99	182.01	8.98
	1	0	2	3	314.06	309.93	4.13	77.2	77.2	0
	1	0	2	4	128.63	115.47	13.16	213.24	194.87	18.37
414	1	0	2	1	336.93	336.51	0.42	94.88	94.88	0
	1	0	2	2	316.63	313.66	2.97	86.31	86.31	0
	1	0	2	3	230.52	230.52	0	114.2	114.2	0
	1	0	2	4	303.05	301.83	1.22	159.98	159.98	0
218	1	0	2	1	121.74	93.06	28.68	181.21	138.56	42.56
	1	0	2	2	260.88	248.82	12.06	71.2	50.27	20.93
	1	0	2	3	214.43	153.85	60.58	188.12	46.93	141.19
	1	0	2	4	88.69	68.08	20.61	157.91	10.58	147.33
176	0	1	2	1	234.14	218.5	15.64	245.5	184.5	61
	0	1	2	2	186.19	145.45	40.69	109.6	36.92	72.68
	0	1	2	3	285.57	265	15.34	200.19	197.5	2.69
	0	1	2	4						
168	0	1	2	1	4.47	3.11	1.36	5.28	0	5.28
	0	1	2	2	62.7	6.65	56.05	43.08	1.97	41.11
	0	1	2	3	43.68	22.51	21.17	89.59	32.41	57.18
	0	1	2	4						
225	0	1	2	1						
	0	1	2	2						

	0	1	2	3						
	0	1	2	4						
245	0	1	2	1	122.68	42.67	80.01	82.3	41.2	41.1
	0	1	2	2	183.7	91.66	92.04	101.97	31.45	70.52
	0	1	2	3	263.2	226.69	36.51	214.63	186.17	28.46
	0	1	2	4	230.14	208.85	21.29	346.62	339.2	7.42
444	1	1	2	1	219.34	118.37	22.93	203.71	184.64	19.07
	1	1	2	2	141.3	191.5	43.74	69.16	214.4	26.4
	1	1	2	3	436.39	404.85	31.54	284.19	178.93	105.26
	1	1	2	4	235.24	135.82	63.52	240.8	57.68	11.48
95	1	1	2	1	165.71	163.51	2.2	84.6	74.1	10.5
	1	1	2	2	389.23	389.13	0.1	395.11	390.71	4.4
	1	1	2	3	96.6	96.6	0	81.77	364.6	2.7
	1	1	2	4	314.56	314.56	0	367.3	67.07	14.7
238	1	1	2	1	41.23	0	41.23	160.01	0	160.01
	1	1	2	2	254.85	143.05	111.8	257.64	197.44	60.2
	1	1	2	3	335.16	265.16	70	178.23	94.27	83.96
	1	1	2	4	212.77	135.53	77.21	105.18	31.98	73.2
281	1	1	2	1	64.65	0	64.65	42.67	0	42.67
	1	1	2	2	1.42	0	1.42	0.76	0	0.76
	1	1	2	3	2.23	0	2.23	1.12	0	1.12
	1	1	2	4						

APPENDIX C. Raw data for the sediment fertilization experiment (Chapter 4). The data represents the values for the 4 replicated plots in each site. Site is the site code; Slope is the littoral slope in m of vertical change per horizontal m; Earea is the effective area in km^2; Fecth is the weighted effective fetch in km; S. depth is the sediment depth in cm; Wc is the percent sediment water content; Org. is the percent organic matter of the dry sediment; TP is the sediment phosphorus concentration in mg g dry wt^{-1}; St is the slope treatment (0, gentle slope; 1, steep slope); Ft is the wave exposure treatment (0, protected; 1, exposed); Depth is the depth treatment (0, 1.0 m; 1, 2.5 m); Plot is the replicate number; Fert indicates that the plot received fertilization; Biomass is teh total submerged biomass in the fertilized plots; Bioper is the overwintering biomass in the fertilized plot; Bioann is the annual biomass in the fertilized plot; and Bioc, Biocp and Bioca are the total, overwintering and annual biomasses in the paired control plot. All plant biomass in g. fresh wt. 0.25 m^{-2}.

Slope	Fetch	Alk	Secchi	Depth	Bioc
0.097	14.54	45	4.3	4.25	1864.318
0.147	2.62	45	3.51	4.25	573.5
0.066	15.67	45	4.3	5.75	507.3351
0.097	14.54	45	4.3	5.25	401.5861
0.042	13.61	32.3	3	3.75	335.7007
0.0207	2.6	39	2.9	2.75	276.835
0.058	1.22	39.83	8	5.75	144.67
0.029	1.16	24	8.5	3.75	83.43182
0.0507	12.61	24	8.5	9.25	80.92679
0.0287	0.866	24.39	6.5	3.25	80.4104
0.095	3.03	23.66	2.8	3.25	40.46339
0.0448	26.15	45	3.51	9.25	29.3
0.008	0.29	50	3.4	5.75	10.9
0.063	4.8	45	5.8	5.75	0
0.121	0.867	31.19	3.1	2.25	0
0.108	18.3	45	3.5	5.25	0
0.0747	17.14	24	8.5	5.25	0
0.05	7.1	45	5.8	4.75	0
0.011	24	26.7	1.6	3.75	0
0.155	0.729	45	4.43	3.25	0
0.0747	17.14	24	8.5	4.75	0
0.294	0.832	18.23	7.8	8.75	0
0.326	0.636	18.23	7.8	3.25	0
0.035	8.3	45	5.8	5.75	0
0.0677	3.13	45	3.5	4.75	0
0.028	10.21	70	4.5	5.75	0
0.0962	0.29	50	3.4	7.75	0
0.093	0.827	39.83	8	4.25	0
0.0448	26.15	45	3.51	5.25	0
0.187	0.219	27.7	3.6	7.75	0
0.155	4.67	70	4.5	6.75	0
0.0076	0.84	31.19	3.1	2.75	0
0.025	0.085	14.6	2	7.75	0
0.042	4.3	45	5.8	5.75	0
0.286	0.085	14.6	2	5.25	0
0.206	0.219	27.7	3.6	3.75	0
0.0346	6.24	23.66	2.8	4.75	0
0.015	8.19	70	4.5	3.75	0
0.012	0.25	78	0.4	3.25	0
0.02	10.3	32.3	3	3.25	0
0.19	0.84	31.19	3.1	7.75	0
0.3	0.39	8.53	3.98	6.75	0
0.0676	0.7719	45	3.5	4.25	0
0.063	15.368	45	3.5	5.75	0
0.095	3.03	23.66	2.8	4.75	0
0.23	5.7	21.7	4.2	2.75	0
0.047	4.47	70	4.5	4.25	0
0.055	2.769	26.7	1.6	2.75	0
0.0378	11.54	45	3.54	4.75	0
0.286	0.085	14.6	2	5.75	0
0.325	0.858	31.19	3.1	3.25	0

0.093	29.17	45	5.8	5.25	0
0.038	0.05	9.83	2.39	3.25	0
0.154	15.616	45	3.5	5.75	0
0.629	0.9	21.6	5.14	6.75	0
0.052	4.3	45	5.8	6.25	0
0.096	0.29	50	3.4	5.25	0
0.325	0.858	31.19	3.1	3.75	0
0.0798	3.7	45	5.8	5.75	0
0.0756	2.064	24.39	6.5	3.75	0
0.093	29.17	45	5.8	5.75	0
0.0034	0.32	78	0.4	2.25	0
0.0751	0.679	35	5.8	5.75	0
0.294	0.832	18.23	7.8	9.75	0
0.0414	1.92	45	5.8	6.25	0
0.108	0.08	7.2	4.2	2.75	0
0.147	2.62	45	3.51	5.25	0
0.253	1.16	45	4.3	6.75	0
0.011	1.826	50.4	2.5	2.75	0
0.0263	2.49	50.4	2.5	4.75	0
0.0346	6.24	23.66	2.8	3.75	0
0.147	23.57	24	8.5	3.75	0
0.0798	3.7	45	5.8	6.25	0
0.088	1.8	45	3.51	5.25	0
0.044	4.6	45	5.8	6.25	0
0.065	13.96	45	3.54	5.25	0
0.044	4.6	45	5.8	5.75	0
0.026	0.48	21.6	5.14	4.75	0
0.079	3.2	45	5.8	5.75	0
0.0358	5.3	50.4	2.5	3.25	0
0.032	14.716	45	2.51	4.25	0
0.0859	2.358	45	3.51	4.75	0
0.108	18.3	45	3.5	5.75	0
0.01	0.157	23.66	2.8	4.25	0
0.036	1.478	23.66	2.8	3.75	0
0.057	1.69	24.39	6.5	5.25	0
0.081	0.05	9.83	2.39	3.25	0
0.042	4.3	45	5.8	8.75	0
0.058	1.28	44.16	0.77	1.75	0
0.0326	24.06	24	8.5	8.25	0
0.086	0.05	9.83	2.39	2.75	0
0.0235	17.48	45	3.54	0.25	0
0.154	6.3	45	4.43	7.75	0
0.206	0.219	27.7	3.6	3.25	0
0.052	4.3	45	5.8	5.75	0
0.05	0.29	50	3.4	6.75	0
0.0126	2.6	39	2.9	3.75	0
0.136	0.39	8.53	3.98	6.75	0
0.0233	4.02	23.66	2.8	4.25	0
0.198	0.39	8.53	3.98	6.75	0
0.2154	5.29	45	5.8	3.25	0
0.0159	0.729	45	2.51	3.75	0
0.088	1.8	45	3.51	5.75	0
0.087	1.35	44.16	0.77	1.75	0
0.0869	21.8	45	3.5	2.25	0
0.155	0.729	45	4.43	2.75	0
0.041	0.871	31.19	3.1	3.25	0

0.0945	0.08	7.2	4.2	5.75	0
0.012	1	70	4.5	4.25	0
0.149	0.085	14.6	2	6.75	0
0.057	1.69	24.39	6.5	5.75	0
0.106	0.085	14.6	2	3.25	0
0.065	13.96	45	3.54	4.75	0
0.052	5.38	24	8.5	6.75	0
0.172	12.29	45	4.3	6.25	0
0.243	0.679	35	5.8	4.25	0
0.043	36.56	45	4.43	5.75	0
0.243	0.679	35	5.8	3.75	0
0.095	3.03	23.66	2.8	3.75	0
0.026	0.39	49	2	4.75	0
0.0031	0.05	9.83	2.39	2.75	0
0.187	0.219	27.7	3.6	8.75	0
0.0817	11.593	45	3.5	4.25	0
0.063	13.06	45	3.5	4.25	0
0.154	6.3	45	4.43	5.75	0
0.3	0.39	8.53	3.98	5.75	0
0.198	0.39	8.53	3.98	6.75	0
0.055	0.708	39.83	8	2.25	0
0.171	5.7	21.7	4.2	5.75	0
0.055	0.708	39.83	8	5.75	0
0.206	0.865	24.39	6.5	8.75	0
0.042	13.61	32.3	3	4.25	0
0.004	36.9	24	8.5	8.25	0
0.105	43	45	3.51	3.25	0
0.0798	3.7	45	5.8	5.25	0
0.009	0.108	39.83	8	7.75	0
0.0326	24.06	24	8.5	7.25	0
0.043	1.2	45	4.43	6.75	0
0.122	0.8	21.6	5.14	4.75	0
0.34	0.08	7.2	4.2	5.75	0
0.0599	1.92	45	5.8	6.25	0
0.0177	8.53	24	8.5	7.75	0
0.3	0.39	8.53	3.98	6.75	0
0.088	1.8	45	3.51	4.25	0
0.0599	1.92	45	5.8	5.25	0
0.043	36.56	45	4.43	5.25	0
0.147	2.62	45	3.51	4.75	0
0.28	15.46	45	4.3	6.75	0
0.042	4.3	45	5.8	6.75	0
0.187	0.219	27.7	3.6	7.25	0
0.03	8.7	21.7	4.2	2.75	0
0.1148	43	45	3.51	3.25	0
0.0711	4.8	45	5.8	6.75	0
0.107	0.05	9.83	2.39	2.75	0
0.127	0.39	8.53	3.98	6.75	0
0.0869	21.8	45	3.5	7.75	0
0.0962	0.29	50	3.4	8.75	0
0.0595	0.9	21.6	5.14	4.75	0
0.155	0.729	45	4.43	3.75	0
0.077	0.047	18.23	7.8	4.75	0
0.0378	11.54	45	4.43	7.75	0
0.0127	4.79	24	8.5	6.25	0
0.326	0.263	27.7	3.6	3.75	0

0.04	10.3	32.3	3	3.75	0
0.042	4.3	45	5.8	5.25	0
0.204	0.022	18.23	7.8	7.75	0
0.085	0.05	9.83	2.39	3.25	0
0.0751	0.679	35	5.8	5.25	0
0.0218	0.29	50	3.4	6.25	0
0.308	0.116	18.23	7.8	8.75	0
0.155	4.67	70	4.5	3.75	0
0.1957	0.085	14.6	2	6.75	0
0.00177	0.0929	44.16	0.77	1.25	645.8815
0.0126	2.6	39	2.9	0.75	420.7867
0.004	36.9	24	8.5	5.75	86.17312
0.004	36.9	24	8.5	2.25	401.7861
0.0031	0.0929	44.16	0.77	1.25	541.9822
0.002	0.52	78	0.4	1.75	565.51
0.0076	0.84	31.19	3.1	1.25	548.5035
0.096	0.29	50	3.4	1.25	202.3064
0.0031	0.0929	44.16	0.77	1.75	243.9315
0.01	1	70	4.5	1.75	1864.318
0.0066	0.0929	44.16	0.77	1.75	84.53309
0.01	1	70	4.5	3.25	2973.187
0.004	36.9	24	8.5	1.75	244.9207
0.0066	0.0929	44.16	0.77	1.25	32.29090
0.004	36.9	24	8.5	2.75	500.5719
0.004	36.9	24	8.5	4.75	287.635
0.0169	53.67	24	8.5	5.75	119.245
0.002	0.52	78	0.4	1.25	1022.275
0.01	1	70	4.5	2.75	3207.34
0.01	1	70	4.5	2.25	2104.44
0.004	36.9	24	8.5	6.75	17.28222
0.0077	2.6	39	2.9	2.75	727.1202
0.0169	53.67	24	8.5	6.25	44.44
0.0127	4.79	24	8.5	5.75	20.2317
0.01	1	70	4.5	3.75	1949.616
0.015	8.19	70	4.5	1.75	324.9049
0.0077	2.6	39	2.9	1.75	1533.884
0.0164	13.61	32.3	3	2.75	0
0.02	10.3	32.3	3	2.75	14.8
0.0095	1.28	44.16	0.77	1.25	218.8413
0.0287	0.866	24.39	6.5	3.75	76.88815
0.096	0.29	50	3.4	1.75	750.5131
0.0146	2.6	39	2.9	3.75	246.0284
0.0218	0.29	50	3.4	0.75	611.3854
0.008	0.29	50	3.4	1.25	231.9716
0.004	36.9	24	8.5	7.25	0
0.004	36.9	24	8.5	3.75	379.5677
0.0077	2.6	39	2.9	2.25	1337.061
0.01	0.157	23.66	2.8	2.75	119.2348
0.0126	2.6	39	2.9	1.75	929.7999
0.015	3.63	21.7	4.2	1.25	180.816
0.0127	4.79	24	8.5	5.25	468.0894
0.0169	53.67	24	8.5	1.25	16.10889
0.0169	53.67	24	8.5	5.25	265.7806
0.004	36.9	24	8.5	3.25	406.945
0.0155	24.19	45	5.8	4.25	124.7507
0.0146	2.6	39	2.9	1.75	664.7877

0.052	4.3	45	5.8	1.25	26.64
0.009448	9.5	21.7	4.2	0.75	17.76
0.0244	34	26.7	1.6	3.25	0
0.004	36.9	24	8.5	6.25	0
0.0095	1.28	44.16	0.77	1.75	186.5516
0.0177	8.53	24	8.5	2.25	3.088695
0.015	8.19	70	4.5	1.25	253.8454
0.023	0.39	49	2	4.25	0
0.004	36.9	24	8.5	4.25	26.9756
0.0076	0.84	31.19	3.1	1.75	1159.655
0.0126	2.6	39	2.9	2.25	1689.592
0.065	0.169	35	5.8	2.75	102.9328
0.017	3	45	4.3	1.25	100.2673
0.004	36.9	24	8.5	5.25	282.2458
0.0164	13.61	32.3	3	2.25	31.99905
0.011	24	26.7	1.6	1.25	197.6164
0.0169	53.67	24	8.5	6.75	80.92679
0.004	36.9	24	8.5	7.75	0
0.023	10.3	32.3	3	3.25	23.68
0.0077	2.6	39	2.9	1.25	1147
0.0169	53.67	24	8.5	1.75	96.41711
0.0127	4.79	24	8.5	0.75	31.42153
0.0169	53.67	24	8.5	2.25	105.4926
0.023	10.3	32.3	3	2.75	30.51825
0.011	1.826	50.4	2.5	2.25	107.0218
0.019	62.7	26.7	1.6	2.75	33.09422
0.0244	34	26.7	1.6	2.75	196.563
0.012	1.43	23.66	2.8	1.25	23.63873
0.012	1.43	23.66	2.8	1.75	41.44159
0.065	0.169	35	5.8	3.25	82.29733
0.008	0.29	50	3.4	1.75	711.8061
0.0076	0.84	31.19	3.1	0.75	0
0.0127	4.79	24	8.5	2.75	462.6551
0.0127	4.79	24	8.5	2.25	539.2376
0.03	8.7	21.7	4.2	3.25	0
0.096	0.29	50	3.4	2.25	626.9595
0.0178	2.6	39	2.9	2.75	512.8477
0.0127	4.79	24	8.5	3.25	1211.291
0.023	0.29	50	3.4	1.25	157.4765
0.0113	0.39	49	2	1.25	978.3138
0.011	24	26.7	1.6	1.75	424.2047
0.0239	0.085	14.6	2	1.25	69.55164
0.026	0.48	21.6	5.14	4.25	271.6516
0.015	3.63	21.7	4.2	1.75	98.37377
0.01	0.157	23.66	2.8	2.25	284.7635
0.0034	0.32	78	0.4	1.25	926.2276
0.0129	3.826	50.4	2.5	2.75	52.67581
0.0244	34	26.7	1.6	2.25	66.33271
0.0159	0.729	45	2.51	3.25	425.4432
0.018	31	26.7	1.6	1.75	187.8223
0.0127	4.79	24	8.5	4.75	914.5393
0.011	24	26.7	1.6	2.75	163.3859
0.0146	2.6	39	2.9	1.25	1002.413
0.0218	0.29	50	3.4	1.25	532.3162
0.0798	3.7	45	5.8	1.25	165.4711
0.0177	8.53	24	8.5	1.75	0

0.0169	53.67	24	8.5	4.75	1146.033
0.1211	20.48	24	8.5	4.75	95.46542
0.016	1.668	50.4	2.5	2.75	291.576
0.0189	9.5	21.7	4.2	1.25	83.18447
0.0127	4.79	24	8.5	1.25	62.12405
0.0215	0.108	39.83	8	1.75	58.40861
0.0216	0.39	49	2	1.25	866.1019
0.01	0.157	23.66	2.8	1.75	41.36778
0.0235	17.48	45	3.54	4.25	598.1256
0.019	62.7	26.7	1.6	1.25	55.15703
0.0378	11.54	45	3.54	3.75	291.3354
0.0169	53.67	24	8.5	2.75	351.097
0.0034	0.32	78	0.4	1.75	407.4226
0.0159	0.729	45	2.51	2.75	664.4401
0.011	24	26.7	1.6	2.25	382.5744
0.026	0.48	21.6	5.14	3.75	562.3779
0.0169	53.67	24	8.5	4.25	2417.752
0.011	1.826	50.4	2.5	1.25	1145.536
0.0129	3.826	50.4	2.5	1.25	1145.455
0.0164	13.61	32.3	3	1.75	141.849
0.0507	12.61	24	8.5	4.25	781.8644
0.0127	4.79	24	8.5	4.25	862.1928
0.0169	53.67	24	8.5	9.25	80.92679
0.0507	12.61	24	8.5	8.75	0
0.0507	12.61	24	8.5	5.75	44.44
0.018	31	26.7	1.6	1.25	11.53065
0.032	14.716	45	2.51	3.75	1038.789
0.011	1.826	50.4	2.5	1.75	1585.484
0.0127	4.79	24	8.5	3.75	1420.841
0.029	1.16	24	8.5	3.25	265.0983
0.0448	26.15	45	3.51	4.25	153.1909
0.0077	2.6	39	2.9	3.25	361.1227
0.022	0.84	24	8.5	1.75	0.7104
0.012	1.43	23.66	2.8	2.25	16.54711
0.026	0.39	49	2	1.75	1557.532
0.015	3.63	21.7	4.2	2.75	50.9764
0.058	1.22	39.83	8	2.25	23.47319
0.015	8.19	70	4.5	2.25	481.449
0.017	3	45	4.3	1.75	112.7136
0.023	6.96	21.7	4.2	2.75	0
0.022	0.84	24	8.5	3.25	282.158
0.0378	11.54	45	3.54	4.25	240.7377
0.017	3	45	4.3	4.75	0
0.0233	4.02	23.66	2.8	1.25	4.73791
0.0178	2.6	39	2.9	3.25	335.7262
0.0127	4.79	24	8.5	1.75	773.0159
0.017	3	45	4.3	2.25	702.8811
0.032	14.716	45	2.51	3.25	926.5278
0.02148	16.5	45	2.51	3.25	535.1303
0.0216	0.39	49	2	4.25	48.21345
0.012	1.43	23.66	2.8	3.25	14.81333
0.0169	53.67	24	8.5	8.75	29.3
0.0126	2.6	39	2.9	2.75	1225.864
0.018	31	26.7	1.6	2.25	227.7178
0.042	13.61	32.3	3	3.25	18.38568
0.038	0.05	9.83	2.39	1.75	936.681

0.0189	9.5	21.7	4.2	1.75	117.4538
0.0155	24.19	45	5.8	1.25	3.946666
0.023	0.39	49	2	3.25	645.6657
0.0235	17.48	45	3.54	3.25	858.6234
0.018	31	26.7	1.6	3.25	0
0.015	3.63	21.7	4.2	2.25	27.25202
0.02148	16.5	45	2.51	2.25	933.0649
0.096	0.29	50	3.4	2.75	1269.12
0.019	62.7	26.7	1.6	2.25	82.73555
0.023	6.96	21.7	4.2	2.25	22.79943
0.023	10.3	32.3	3	2.25	77.53394
0.0326	24.06	24	8.5	1.25	163.4366
0.029	1.16	24	8.5	0.75	24.35149
0.0239	0.085	14.6	2	3.25	7.269092
0.0239	0.085	14.6	2	1.75	99.36229
0.277	10.8	45	3.54	4.25	62.43206
0.0169	53.67	24	8.5	3.25	144.6957
0.02	10.3	32.3	3	2.25	12.22604
0.0166	0.39	49	2	1.75	1841.339
0.0378	11.54	45	3.54	3.25	383.9544
0.016	1.668	50.4	2.5	0.75	576.1368
0.0129	3.826	50.4	2.5	1.75	1621.337
0.0169	53.67	24	4.25	9.75	29.3
0.0169	53.67	24	8.5	8.25	22.22
0.0169	53.67	24	8.5	7.75	44.44
0.0216	0.39	49	2	2.25	908.1686
0.0164	13.61	32.3	3	1.25	124.133
0.0235	17.48	45	3.54	3.75	346.4406
0.023	6.96	21.7	4.2	1.25	0
0.0216	0.39	49	2	1.75	1331.912
0.02148	16.5	45	2.51	2.75	387.8549
0.023	0.39	49	2	3.75	116.4487
0.017	3	45	4.3	4.25	325.9444
0.0589	0.679	35	5.8	1.25	641.6347
0.0169	53.67	24	8.5	3.75	532.7136
0.0448	26.15	45	3.51	3.75	21.58048
0.011	24	26.7	1.6	3.25	32.19500
0.0235	17.48	45	3.54	2.75	996.2445
0.0129	3.826	50.4	2.5	2.25	1109.933
0.0178	2.6	39	2.9	1.75	1267.258
0.0216	0.39	49	2	0.75	484.3366
0.046	4.02	23.66	2.8	0.75	71.04
0.008	0.29	50	3.4	2.25	1651.206
0.0177	8.53	24	8.5	0.75	0
0.022	0.84	24	8.5	1.25	2.22
0.032	14.716	45	2.51	2.75	158.9895
0.0178	2.6	39	2.9	0.75	507.0095
0.023	0.29	50	3.4	1.75	122.9955
0.0155	24.19	45	5.8	3.75	630.4027
0.02148	16.5	45	2.51	1.75	1215.774
0.0218	0.29	50	3.4	1.75	888.2958
0.02	10.3	32.3	3	1.75	40.19854
0.043	6.96	21.7	4.2	0.75	0
0.017	3	45	4.3	3.75	2578.683
0.0177	8.53	24	8.5	2.75	10.06806
0.043	36.56	45	4.43	1.25	191.5284

0.0159	0.729	45	2.51	1.75	404.4095
0.023	0.39	49	2	1.75	1451.205
0.024447	1.478	23.66	2.8	1.25	47.40104
0.017	3	45	4.3	2.75	1436.757
0.1211	20.48	24	8.5	4.25	16.18536
0.0076	0.84	31.19	3.1	2.25	341.1191
0.0458	2.56	45	5.8	4.75	418.7613
0.0155	24.19	45	5.8	4.75	250.0454
0.0178	2.6	39	2.9	1.25	839.7362
0.0244	34	26.7	1.6	1.75	21.45926
0.03	8.7	21.7	4.2	2.25	13.32
0.016	1.668	50.4	2.5	2.25	760.5758
0.026	0.48	21.6	5.14	3.25	316.879
0.0507	12.61	24	8.5	5.25	22.22
0.0235	17.48	45	3.54	2.25	334.0832
0.0146	2.6	39	2.9	2.75	217.0366
0.0178	2.6	39	2.9	2.25	1218.882
0.0282	10.21	70	4.5	2.25	0
0.0282	10.21	70	4.5	1.75	0
0.025599	10.21	70	4.5	1.25	0
0.023	6.96	21.7	4.2	1.75	4.933332
0.02	10.3	32.3	3	1.25	59.4636
0.026	0.48	21.6	5.14	2.75	316.4101
0.019	62.7	26.7	1.6	1.75	105.1345
0.277	10.8	45	3.54	1.25	10.92923
0.023	0.39	49	2	2.25	1523.615
0.0396	4.05	50.4	2.5	3.25	0
0.0277	18.18	45	3.51	2.25	416.7745
0.017	3	45	4.3	3.25	2392.749
0.023	0.39	49	2	2.75	1164.211
0.023	10.3	32.3	3	1.75	8.054447
0.0282	10.21	70	4.5	2.75	0
0.018	31	26.7	1.6	2.75	63.37682
0.016	1.668	50.4	2.5	1.75	1340.003
0.022	0.84	24	8.5	2.75	132.3719
0.052	5.38	24	8.5	6.25	0
0.0169	53.67	24	8.5	7.25	8.888
0.0279	1.69	24.39	6.5	1.75	0
0.0279	1.69	24.39	6.5	2.25	0
0.015	3.63	21.7	4.2	3.25	20.13612
0.277	10.8	45	3.54	2.25	46.8
0.0346	6.24	23.66	2.8	2.25	35.52000
0.0146	2.6	39	2.9	2.25	587.8938
0.0177	8.53	24	8.5	3.25	8.88
0.093	0.827	39.83	8	1.75	29.42569
0.096	0.29	50	3.4	3.25	1503.745
0.277	10.8	45	3.54	2.75	10.02708
0.0239	0.085	14.6	2	2.75	13.21078
0.0166	0.39	49	2	2.25	2753.035
0.0279	1.69	24.39	6.5	2.75	0
0.035	8.3	45	5.8	3.25	113.0115
0.042	4.3	45	5.8	1.75	60.86763
0.022	0.84	24	8.5	2.25	34.48337
0.0282	10.21	70	4.5	4.25	0
0.0282	10.21	70	4.5	5.25	0
0.0244	34	26.7	1.6	1.25	44.4

0.01	0.157	23.66	2.8	3.25	146.8328
0.0282	10.21	70	4.5	3.75	0
0.0282	10.21	70	4.5	4.75	0
0.0215	0.108	39.83	8	1.25	113.3104
0.0287	0.866	24.39	6.5	2.75	128.3866
0.026	0.48	21.6	5.14	1.25	133.3794
0.0207	2.6	39	2.9	3.25	483.8552
0.0282	10.21	70	4.5	3.25	0
0.0159	0.729	45	2.51	1.25	124.32
0.026	0.48	21.6	5.14	1.75	272.7225
0.0235	17.48	45	3.54	1.75	25.07294
0.0277	18.18	45	3.51	1.75	34.45278
0.0166	0.39	49	2	2.75	3399.296
0.0756	2.064	24.39	6.5	2.25	5.92
0.0277	18.18	45	3.51	1.25	98.58032
0.0207	2.6	39	2.9	2.25	785.0978
0.04	10.3	32.3	3	3.25	34.09208
0.0516	0.679	35	5.8	3.25	5.92
0.02148	16.5	45	2.51	1.25	551.1365
0.02148	16.5	45	2.51	3.75	307.7441
0.0448	26.15	45	3.51	4.75	26.9756
0.277	10.8	45	3.54	3.25	112.4009
0.0233	4.02	23.66	2.8	1.75	181.3507
0.121	0.867	31.19	3.1	1.25	64.0642
0.029	1.16	24	8.5	2.25	12.39146
0.058	1.22	39.83	8	3.25	83.90446
0.0519	1.69	24.39	6.5	1.25	0
0.0326	24.06	24	8.5	1.75	41.44
0.0263	2.49	50.4	2.5	1.75	21.312
0.277	10.8	45	3.54	1.75	21.2
0.0189	9.5	21.7	4.2	2.25	125.9701
0.01	0.157	23.66	2.8	3.75	97.88853
0.038	0.05	9.83	2.39	2.25	500.7469
0.012	1.43	23.66	2.8	2.75	19.04571
0.0215	0.108	39.83	8	0.75	129.2505
0.016	1.668	50.4	2.5	3.25	0
0.051	0.08	7.2	4.2	2.75	14.8
0.029	1.16	24	8.5	1.25	78.3457
0.029	1.16	24	8.5	2.75	33.89571
0.0507	12.61	24	8.5	0.75	0
0.0177	8.53	24	8.5	4.25	44.44
0.0414	1.92	45	5.8	1.25	97.2178
0.0277	18.18	45	3.51	2.75	772.3961
0.035	8.3	45	5.8	3.75	66.82472
0.05	0.29	50	3.4	1.25	45.08308
0.042	0.6	21.6	5.14	1.25	23.68
0.0218	0.29	50	3.4	2.25	1135.008
0.0263	2.49	50.4	2.5	2.25	21.17694
0.036	1.478	23.66	2.8	1.75	109.7024
0.0346	6.24	23.66	2.8	1.75	30.192
0.0711	4.8	45	5.8	4.25	8.991865
0.0326	24.06	24	8.5	2.25	55.19885
0.0507	12.61	24	8.5	4.75	7.406668
0.0516	0.679	35	5.8	2.75	5.214489
0.0711	4.8	45	5.8	3.75	13.4878
0.012	0.25	78	0.4	2.75	0

0.008	0.29	50	3.4	2.75	2254.449
0.0414	1.92	45	5.8	1.75	224.2926
0.0277	18.18	45	3.51	3.25	230.5327
0.016	1.668	50.4	2.5	1.25	931.3834
0.065	0.169	35	5.8	2.25	82.54717
0.0507	12.61	24	8.5	3.25	29.36656
0.032	14.716	45	2.51	2.25	205.3928
0.0812	1.545	24.39	6.5	3.25	106.0034
0.0756	2.064	24.39	6.5	1.75	0
0.0239	0.085	14.6	2	2.25	57.84201
0.058	1.22	39.83	8	7.25	0
0.035	8.3	45	5.8	2.25	79.98961
0.096	0.29	50	3.4	3.75	1146.465
0.0277	18.18	45	3.51	3.75	26.9756
0.277	10.8	45	3.54	3.75	6.225138
0.066	15.67	45	4.3	5.25	0
0.277	10.8	45	3.54	4.75	0
0.253	1.019	45	2.51	6.25	14.81333
0.253	1.019	45	2.51	5.75	0
0.052	11.23	21.7	4.2	2.75	0
0.052	11.23	21.7	4.2	1.75	82.73555
0.052	11.23	21.7	4.2	2.25	29.6
0.029	1.16	24	8.5	1.75	15.04283
0.023	0.29	50	3.4	2.25	166.06
0.035	8.3	45	5.8	2.75	225.6695
0.096	0.29	50	3.4	4.25	546.9573
0.04	10.3	32.3	3	2.25	21.312
0.0599	1.92	45	5.8	1.25	62.5808
0.023	10.3	32.3	3	1.25	35.52
0.0166	0.39	49	2	3.75	685.0447
0.036	1.478	23.66	2.8	3.25	310.7197
0.1067	0.085	14.6	2	0.75	88.88
0.0177	8.53	24	8.5	1.25	0
0.0177	8.53	24	8.5	3.75	46.82405
0.041	0.871	31.19	3.1	1.25	278.1986
0.085	3.29	19.2	3.2	0.75	0
0.085	3.29	19.2	3.2	2.75	0
0.085	3.29	19.2	3.2	2.25	0
0.085	3.29	19.2	3.2	1.75	0
0.085	3.29	19.2	3.2	1.25	0
0.0378	11.54	45	3.54	2.75	64.60654
0.052	4.3	45	5.8	1.75	27.84338
0.0595	0.9	21.6	5.14	1.25	6.038442
0.022	0.84	24	8.5	0.75	0
0.0747	17.14	24	8.5	0.75	0
0.0207	2.6	39	2.9	3.75	46.82405
0.05	7.1	45	5.8	1.75	69.13872
0.008	0.29	50	3.4	3.25	2447.067
0.034	4.13	70	4.5	3.25	1659.835
0.081	0.05	9.83	2.39	1.25	8.343183
0.044	4.6	45	5.8	2.75	790.8824
0.0812	1.545	24.39	6.5	3.75	5.92
0.04	10.3	32.3	3	2.75	195.4058
0.0378	11.54	45	3.54	1.75	10.14857
0.008	0.29	50	3.4	5.25	0
0.04	10.3	32.3	3	1.75	10.656

0.036	1.478	23.66	2.8	2.25	21.30755
0.0676	0.7719	45	3.5	3.75	211.7146
0.055	0.708	39.83	8	3.25	26.69687
0.0751	0.679	35	5.8	1.25	17.76
0.01	0.157	23.66	2.8	1.25	0
0.0346	6.24	23.66	2.8	1.25	10.05609
0.0166	0.39	49	2	3.25	3116.156
0.042	4.3	45	5.8	2.25	215.863
0.036	1.478	23.66	2.8	2.75	5.746337
0.026	0.39	49	2	2.75	1995.156
0.035	8.3	45	5.8	1.25	23.68
0.05	7.1	45	5.8	1.25	11.84
0.038	0.05	9.83	2.39	2.75	10.42898
0.066	15.67	45	4.3	4.25	157.4936
0.044	10.538	45	3.5	3.25	0
0.0216	0.39	49	2	3.75	754.105
0.1067	0.085	14.6	2	2.75	0
0.0458	2.56	45	5.8	5.25	13.4878
0.055	2.769	26.7	1.6	2.25	21.13953
0.0448	26.15	45	3.51	2.75	583.4741
0.044	10.538	45	3.5	2.75	0
0.0676	0.7719	45	3.5	3.25	173.1685
0.0507	12.61	24	8.5	3.75	71.15221
0.0358	5.3	50.4	2.5	2.75	266.5354
0.057	1.69	24.39	6.5	2.75	23.68
0.066	15.67	45	4.3	1.25	71.04
0.0711	4.8	45	5.8	1.25	670.3525
0.042	4.3	45	5.8	1.25	35.52
0.03	5.09	45	5.8	2.25	211.7317
0.05	7.1	45	5.8	2.75	779.3134
0.032	14.716	45	2.51	1.25	0
0.121	0.867	31.19	3.1	1.75	745.6775
0.0458	2.56	45	5.8	2.25	90.8106
0.0346	6.24	23.66	2.8	2.75	20.72
0.0458	2.56	45	5.8	3.25	297.8413
0.05	0.29	50	3.4	3.75	36.7082
0.065	0.169	35	5.8	1.25	83.34522
0.0516	0.679	35	5.8	2.25	33.64831
0.042	0.6	21.6	5.14	1.75	96.26123
0.052	4.3	45	5.8	3.75	146.5993
0.0207	2.6	39	2.9	1.75	1447.473
0.03	8.7	21.7	4.2	1.75	11.50635
0.026	0.39	49	2	2.25	2039.782
0.0676	0.7719	45	3.5	1.25	5.074284
0.121	0.867	31.19	3.1	2.75	9.866668
0.0326	24.06	24	8.5	2.75	51.49848
0.044	10.538	45	3.5	4.25	0
0.044	10.538	45	3.5	3.75	0
0.0287	0.866	24.39	6.5	1.25	24.864
0.0326	24.06	24	8.5	4.75	11.56097
0.0458	2.56	45	5.8	4.25	313.6038
0.052	5.38	24	8.5	0.75	10.656
0.012	0.25	78	0.4	1.25	952.5882
0.0396	4.05	50.4	2.5	2.75	21.70666
0.057	1.69	24.39	6.5	3.25	21.85846
0.0817	11.593	45	3.5	2.75	28.416

0.051	0.08	7.2	4.2	2.25	68.91396
0.012	0.25	78	0.4	2.25	0
0.065	0.169	35	5.8	1.75	176.6761
0.042	0.6	21.6	5.14	2.25	179.3379
0.044	4.6	45	5.8	2.25	516.3403
0.0762	1.633	23.66	2.8	1.25	5.92
0.0448	26.15	45	3.51	1.25	21.312
0.008	0.29	50	3.4	4.25	2890.234
0.05	7.1	45	5.8	2.25	825.8263
0.0378	11.54	45	3.54	2.25	11.84
0.051	0.08	7.2	4.2	1.25	21.312
0.008	0.29	50	3.4	3.75	3046.607
0.0448	26.15	45	3.51	2.25	488.6692
0.093	0.827	39.83	8	2.25	29.6
0.0358	5.3	50.4	2.5	2.25	1232.157
0.096	0.29	50	3.4	4.75	20.2317
0.0218	0.29	50	3.4	5.25	116.4
0.0177	8.53	24	8.5	5.25	14.81333
0.026	0.48	21.6	5.14	2.25	231.0963
0.073	1.2	45	4.43	1.25	13.32
0.052	5.38	24	8.5	1.25	66.90084
0.0177	8.53	24	8.5	4.75	17.776
0.0287	0.866	24.39	6.5	2.25	30.75195
0.03	5.09	45	5.8	1.75	89.04449
0.0126	2.6	39	2.9	3.25	512.5502
0.052	5.38	24	8.5	5.75	20.2317
0.035	8.3	45	5.8	1.75	10.06806
0.044	4.6	45	5.8	1.75	314.5602
0.023	0.29	50	3.4	2.75	429.9627
0.0326	24.06	24	8.5	4.25	73.4164
0.05	7.1	45	5.8	3.25	752.4418
0.015	8.19	70	4.5	2.75	266.7497
0.0458	2.56	45	5.8	2.75	400.8398
0.066	15.67	45	4.3	2.25	149.4121
0.066	15.67	45	4.3	3.75	0
0.121	0.867	31.19	3.1	0.75	0
0.023	0.29	50	3.4	5.25	97.88853
0.042	0.6	21.6	5.14	4.75	20.2317
0.058	1.22	39.83	8	6.75	0
0.0507	12.61	24	8.5	2.75	114.6449
0.093	29.17	45	5.8	3.25	700.6174
0.063	4.8	45	5.8	1.25	0
0.042	0.6	21.6	5.14	2.75	101.9406
0.0218	0.29	50	3.4	4.25	905.4103
0.093	0.827	39.83	8	3.25	0
0.0751	0.679	35	5.8	1.75	30.44571
0.0287	0.866	24.39	6.5	1.75	23.088
0.044	4.6	45	5.8	3.25	638.4902
0.055	0.708	39.83	8	2.25	4.469374
0.0507	12.61	24	8.5	1.25	11.50635
0.042	13.61	32.3	3	1.25	40.27224
0.0589	0.679	35	5.8	2.75	722.2453
0.0762	1.633	23.66	2.8	2.75	0
0.0589	0.679	35	5.8	3.75	160.0037
0.0216	0.39	49	2	3.25	892.1786
0.0233	4.02	23.66	2.8	2.25	122.5998

0.0177	8.53	24	8.5	5.75	0
0.0218	0.29	50	3.4	2.75	1025.135
0.063	4.8	45	5.8	2.25	0
0.063	15.368	45	3.5	3.75	0
0.121	0.867	31.19	3.1	2.25	415.9162
0.052	5.38	24	8.5	1.75	131.2217
0.055	2.769	26.7	1.6	1.75	65.12
0.063	4.8	45	5.8	0.75	0
0.0458	2.56	45	5.8	1.75	20.29714
0.0414	1.92	45	5.8	2.75	519.5665
0.0448	26.15	45	3.51	1.75	215.8524
0.035	8.3	45	5.8	4.25	261.6672
0.0155	24.19	45	5.8	2.25	354.3262
0.0676	0.7719	45	3.5	2.75	600.9425
0.058	1.22	39.83	8	3.75	62.75893
0.0458	2.56	45	5.8	3.75	217.7422
0.0155	24.19	45	5.8	3.25	862.1663
0.05	7.1	45	5.8	3.75	55.57277
0.063	4.8	45	5.8	2.75	0
0.0326	24.06	24	8.5	3.75	13.4878
0.0677	3.13	45	3.5	1.25	4.44
0.041	0.871	31.19	3.1	1.75	552.6263
0.102	3.29	19.2	3.2	2.25	0
0.102	3.29	19.2	3.2	0.75	0
0.102	3.29	19.2	3.2	1.25	0
0.102	3.29	19.2	3.2	3.25	0
0.102	3.29	19.2	3.2	2.75	0
0.102	3.29	19.2	3.2	1.75	0
0.0218	0.29	50	3.4	5.75	50.8
0.0218	0.29	50	3.4	4.75	2023.292
0.0507	12.61	24	8.5	2.25	39.072
0.051	0.08	7.2	4.2	1.75	37.46611
0.0589	0.679	35	5.8	1.75	321.4629
0.0762	1.633	23.66	2.8	1.75	24.42
0.063	4.8	45	5.8	0.25	0
0.063	4.8	45	5.8	1.75	0
0.063	15.368	45	3.5	4.25	0
0.063	13.06	45	3.5	1.25	0
0.0458	2.56	45	5.8	1.25	30.51825
0.032	14.716	45	2.51	1.75	5.074284
0.0146	2.6	39	2.9	3.25	125.5756
0.085	0.05	9.83	2.39	1.25	60.384
0.0812	1.545	24.39	6.5	2.25	0
0.063	13.06	45	3.5	2.75	0
0.0589	0.679	35	5.8	3.25	22.22
0.0817	11.593	45	3.5	3.25	75.78518
0.097	14.54	45	4.3	4.75	220.4819
0.063	4.8	45	5.8	4.25	207.9404
0.0516	0.679	35	5.8	1.75	0
0.066497	1.633	23.66	2.8	0.75	40.848
0.095	3.03	23.66	2.8	1.75	29.6
0.0798	3.7	45	5.8	1.75	119.4446
0.042	13.61	32.3	3	2.25	40.27224
0.034	4.13	70	4.5	3.75	657.4429
0.052	4.3	45	5.8	2.25	341.5621
0.0177	8.53	24	8.5	6.75	0

0.066	15.67	45	4.3	1.75	77.68124
0.079	3.2	45	5.8	1.75	53.28
0.068080	4.13	70	4.5	1.75	477.9618
0.0859	2.358	45	3.51	2.25	20.13612
0.034	4.13	70	4.5	2.75	1180.128
0.03	5.09	45	5.8	2.75	948.4214
0.155	0.729	45	4.43	2.25	0
0.0396	4.05	50.4	2.5	2.25	66.70853
0.052	5.38	24	8.5	2.75	317.5178
0.077	0.047	18.23	7.8	3.25	30.75195
0.0599	1.92	45	5.8	1.75	359.3933
0.0396	4.05	50.4	2.5	1.25	96.56666
0.063	15.368	45	3.5	3.25	0
0.055	0.708	39.83	8	4.75	338.936
0.055	0.708	39.83	8	4.25	124.8641
0.043	36.56	45	4.43	3.25	2119.052
0.097	14.54	45	4.3	3.25	1046.116
0.1211	20.48	24	8.5	3.75	4.444
0.095	3.03	23.66	2.8	1.25	0
0.057	1.69	24.39	6.5	2.25	0
0.052	5.38	24	8.5	5.25	16.18536
0.065	13.96	45	3.54	2.25	121.6685
0.081	0.05	9.83	2.39	2.75	0
0.012	0.25	78	0.4	1.75	222.3718
0.065	13.96	45	3.54	1.75	26.64
0.052	5.38	24	8.5	4.25	20.2317
0.058	1.22	39.83	8	2.75	11.84
0.065	13.96	45	3.54	3.25	381.8573
0.052	5.38	24	8.5	2.25	109.5837
0.063	13.06	45	3.5	1.75	0
0.055	0.708	39.83	8	2.75	24.42000
0.052	4.3	45	5.8	2.75	877.4108
0.0507	12.61	24	8.5	1.75	13.32
0.0677	3.13	45	3.5	1.75	76.72282
0.0516	0.679	35	5.8	1.25	13.9053
0.0326	24.06	24	8.5	3.25	20.2317
0.0711	4.8	45	5.8	1.75	487.66
0.057	1.69	24.39	6.5	1.75	0
0.042	13.61	32.3	3	1.75	99.30644
0.0218	0.29	50	3.4	3.75	1099.105
0.03	5.09	45	5.8	4.75	870.0231
0.063	4.8	45	5.8	5.25	0
0.0869	21.8	45	3.5	5.25	0
0.0869	21.8	45	3.5	6.25	0
0.0869	21.8	45	3.5	7.25	0
0.063	15.368	45	3.5	2.75	0
0.0869	21.8	45	3.5	5.75	0
0.0869	21.8	45	3.5	6.75	0
0.0155	24.19	45	5.8	2.75	770.3682
0.042	0.6	21.6	5.14	3.75	82.82166
0.0747	17.14	24	8.5	1.25	0
0.052	4.3	45	5.8	3.25	310.3512
0.0326	24.06	24	8.5	5.25	26.664
0.052	5.38	24	8.5	4.75	16.18536
0.042	4.3	45	5.8	2.75	1479.416
0.026	0.39	49	2	4.25	0

0.0589	0.679	35	5.8	5.25	0
0.0346	6.24	23.66	2.8	3.25	0
0.0589	0.679	35	5.8	4.75	40.46339
0.0589	0.679	35	5.8	4.25	44.44
0.0396	4.05	50.4	2.5	1.75	161.2522
0.097	14.54	45	4.3	2.75	872.3434
0.052	5.38	24	8.5	3.75	160.7395
0.088	0.16	27.7	3.6	1.25	35.52000
0.063	13.06	45	3.5	2.25	0
0.0711	4.8	45	5.8	4.75	120.3742
0.0945	0.08	7.2	4.2	1.25	0
0.079	3.2	45	5.8	2.25	24.35149
0.03	5.09	45	5.8	5.25	114.7389
0.042	0.6	21.6	5.14	3.25	101.4704
0.05	7.1	45	5.8	4.25	8.888
0.079	3.2	45	5.8	4.75	144.7119
0.0747	17.14	24	8.5	1.75	0
0.0812	1.545	24.39	6.5	1.75	0
0.0676	0.7719	45	3.5	1.75	28.85999
0.041	0.871	31.19	3.1	2.25	557.399
0.0812	1.545	24.39	6.5	2.75	50.47247
0.0762	1.633	23.66	2.8	2.25	16.18536
0.0414	1.92	45	5.8	2.25	569.1732
0.055	0.708	39.83	8	3.75	116.4903
0.086	0.05	9.83	2.39	2.25	0
0.077	0.047	18.23	7.8	2.75	35.34562
0.043	36.56	45	4.43	2.75	1667.674
0.093	29.17	45	5.8	2.75	431.6918
0.0817	11.593	45	3.5	2.25	41.44
0.088	0.16	27.7	3.6	3.25	31.72
0.026	0.39	49	2	3.25	1027.581
0.008	0.29	50	3.4	4.75	508.4375
0.1067	0.085	14.6	2	1.25	71.104
0.0235	17.48	45	3.54	1.25	156.2555
0.066	15.67	45	4.3	4.75	26.9756
0.052	11.23	21.7	4.2	1.25	0
0.097	14.54	45	4.3	3.75	1460.759
0.066	15.67	45	4.3	2.75	293.6565
0.058	1.28	44.16	0.77	0.75	0
0.058	1.28	44.16	0.77	0.25	0
0.058	1.28	44.16	0.77	1.25	0
0.077	0.047	18.23	7.8	2.25	46.62548
0.035	8.3	45	5.8	4.75	65.07417
0.0031	0.05	9.83	2.39	2.25	0
0.0031	0.05	9.83	2.39	1.25	0
0.0599	1.92	45	5.8	2.25	1069.262
0.042	0.6	21.6	5.14	4.25	117.4662
0.079	3.2	45	5.8	2.75	72.66957
0.121	0.867	31.19	3.1	1.25	32.56
0.03	5.09	45	5.8	3.25	1552.963
0.107	0.05	9.83	2.39	1.25	0
0.107	0.05	9.83	2.39	2.25	0
0.0945	0.08	7.2	4.2	4.25	0
0.0945	0.08	7.2	4.2	3.25	0
0.0945	0.08	7.2	4.2	4.75	0
0.0945	0.08	7.2	4.2	5.25	0

0.0945	0.08	7.2	4.2	2.75	0
0.0945	0.08	7.2	4.2	3.75	0
0.1067	0.085	14.6	2	2.25	29.62666
0.0595	0.9	21.6	5.14	1.75	382.3881
0.088	0.16	27.7	3.6	2.75	31.96800
0.052	5.38	24	8.5	3.25	318.6018
0.155	0.729	45	4.43	1.75	0
0.079	3.2	45	5.8	3.25	57.74092
0.0218	0.29	50	3.4	3.25	230.5497
0.108	0.08	7.2	4.2	1.25	0
0.108	0.08	7.2	4.2	2.25	0
0.253	1.16	45	4.3	2.25	0
0.1148	43	45	3.51	0.25	0
0.1148	43	45	3.51	2.75	0
0.066	15.67	45	4.3	3.25	85.6908
0.0676	0.7719	45	3.5	2.25	35.52
0.092440	1.69	24.39	6.5	0.25	0
0.0751	0.679	35	5.8	2.75	0
0.077	0.047	18.23	7.8	4.25	146.8328
0.077	0.047	18.23	7.8	3.75	169.1117
0.0751	0.679	35	5.8	2.25	26.64
0.085	0.05	9.83	2.39	2.25	26.64
0.087	1.35	44.16	0.77	0.25	0
0.087	1.35	44.16	0.77	1.25	0
0.087	1.35	44.16	0.77	0.75	0
0.0677	3.13	45	3.5	2.25	666.5685
0.107	0.05	9.83	2.39	0.75	0
0.243	0.679	35	5.8	1.75	8.88
0.077	0.047	18.23	7.8	1.25	13.42408
0.079	3.2	45	5.8	5.25	72.47645
0.079	3.2	45	5.8	4.25	457.5496
0.0711	4.8	45	5.8	5.25	146.8328
0.052	4.3	45	5.8	4.75	0
0.063	15.368	45	3.5	4.75	0
0.0414	1.92	45	5.8	5.75	0
0.108	0.08	7.2	4.2	0.75	0
0.0945	0.08	7.2	4.2	2.25	0
0.057	1.69	24.39	6.5	1.25	0
0.057	1.69	24.39	6.5	0.75	0
0.0358	5.3	50.4	2.5	1.75	745.172
0.108	0.08	7.2	4.2	1.75	0
0.107	0.05	9.83	2.39	1.75	0
0.1211	20.48	24	8.5	3.25	0
0.105	43	45	3.51	0.75	0
0.105	43	45	3.51	2.75	0
0.0448	26.15	45	3.51	3.25	421.1797
0.05	0.29	50	3.4	3.25	16.18536
0.015	8.19	70	4.5	3.25	0
0.047	4.47	70	4.5	1.25	60.69509
0.063	13.06	45	3.5	3.75	0
0.063	13.06	45	3.5	3.25	0
0.122	0.8	21.6	5.14	3.75	206.0405
0.0263	2.49	50.4	2.5	3.25	29.62666
0.0155	24.19	45	5.8	1.75	58.73312
0.0945	0.08	7.2	4.2	0.75	0
0.0812	1.545	24.39	6.5	1.25	0

0.0812	1.545	24.39	6.5	0.75	0
0.065	13.96	45	3.54	2.75	825.7039
0.041	0.871	31.19	3.1	2.75	75.7087
0.081	0.05	9.83	2.39	1.75	70.68913
0.0326	24.06	24	8.5	6.25	0
0.0326	24.06	24	8.5	7.75	0
0.108	18.3	45	3.5	4.25	0
0.108	18.3	45	3.5	2.75	0
0.097	14.54	45	4.3	1.75	84.84856
0.0945	0.08	7.2	4.2	1.75	0
0.0677	3.13	45	3.5	3.25	1909.089
0.0599	1.92	45	5.8	3.75	1014.717
0.0677	3.13	45	3.5	4.25	0
0.063	4.8	45	5.8	4.75	0
0.108	0.08	7.2	4.2	0.25	0
0.097	14.54	45	4.3	1.25	0
0.0817	11.593	45	3.5	1.75	41.44
0.081	0.05	9.83	2.39	2.25	35.52000
0.105	43	45	3.51	1.75	0
0.105	43	45	3.51	0.25	0
0.108	18.3	45	3.5	3.75	0
0.034	4.13	70	4.5	2.25	1212.049
0.122	0.8	21.6	5.14	2.75	169.1117
0.108	18.3	45	3.5	2.25	0
0.0677	3.13	45	3.5	2.75	1500.725
0.0711	4.8	45	5.8	2.75	758.9143
0.105	43	45	3.51	2.25	0
0.093	29.17	45	5.8	2.25	55.15703
0.088	1.8	45	3.51	1.25	47.36
0.108329	1.545	24.39	6.5	0.25	0
0.065	13.96	45	3.54	3.75	0
0.093	0.827	39.83	8	2.75	49.06705
0.0326	24.06	24	8.5	6.75	0
0.0263	2.49	50.4	2.5	2.75	13.32
0.0945	0.08	7.2	4.2	0.25	0
0.088	0.16	27.7	3.6	1.75	60.384
0.105	43	45	3.51	1.25	0
0.055	0.708	39.83	8	5.25	303.4368
0.122	0.8	21.6	5.14	4.25	147.0655
0.058	1.22	39.83	8	6.25	0
0.058	1.22	39.83	8	4.25	115.8246
0.03	5.09	45	5.8	1.25	37.1622
0.044	4.6	45	5.8	3.75	567.8478
0.147	23.57	24	8.5	1.25	0
0.0859	2.358	45	3.51	1.25	0
0.093	29.17	45	5.8	1.25	35.52
0.0677	3.13	45	3.5	3.75	729.3863
0.0817	11.593	45	3.5	3.75	338.9583
0.0711	4.8	45	5.8	5.75	0
0.043	1.2	45	4.43	2.75	0
0.065	13.96	45	3.54	4.25	0
0.108	18.3	45	3.5	3.25	0
0.147	23.57	24	8.5	1.75	0
0.147	23.57	24	8.5	2.75	0
0.108	18.3	45	3.5	4.75	0
0.0126	2.6	39	2.9	1.25	53.28

0.1148	43	45	3.51	0.75	0
0.1148	43	45	3.51	1.25	0
0.1148	43	45	3.51	2.25	0
0.0711	4.8	45	5.8	3.25	78.50728
0.0859	2.358	45	3.51	1.75	13.42408
0.0751	0.679	35	5.8	4.25	26.9756
0.047	4.47	70	4.5	3.75	0
0.05	0.29	50	3.4	2.75	97.56503
0.086	0.05	9.83	2.39	1.25	0
0.086	0.05	9.83	2.39	0.75	0
0.086	0.05	9.83	2.39	1.75	0
0.0216	0.39	49	2	2.75	755.8432
0.0326	24.06	24	8.5	5.75	0
0.063	4.8	45	5.8	3.25	0
0.043	1.2	45	4.43	1.75	324.0367
0.326	0.636	18.23	7.8	2.75	0
0.326	0.636	18.23	7.8	0.75	0
0.326	0.636	18.23	7.8	1.75	0
0.183	3.29	19.2	3.2	1.25	0
0.183	3.29	19.2	3.2	0.75	0
0.183	3.29	19.2	3.2	2.25	0
0.183	3.29	19.2	3.2	1.75	0
0.183	3.29	19.2	3.2	2.75	0
0.172	12.29	45	4.3	1.75	0
0.1067	0.085	14.6	2	1.75	64.2846
0.05	0.29	50	3.4	1.75	14.90694
0.0747	17.14	24	8.5	2.25	0
0.023	0.29	50	3.4	4.75	8.888
0.0751	0.679	35	5.8	3.25	17.76
0.0798	3.7	45	5.8	3.25	1849.623
0.0414	1.92	45	5.8	4.75	97.88853
0.058	1.22	39.83	8	1.75	0
0.1211	20.48	24	8.5	2.25	0
0.171	5.7	21.7	4.2	3.25	0
0.171	5.7	21.7	4.2	4.25	0
0.0711	4.8	45	5.8	2.25	582.1601
0.0747	17.14	24	8.5	2.75	0
0.0233	4.02	23.66	2.8	2.75	305.2076
0.1211	20.48	24	8.5	1.25	0
0.0263	2.49	50.4	2.5	3.75	11.11
0.052	4.3	45	5.8	4.25	11.56097
0.147	23.57	24	8.5	0.25	0
0.0859	2.358	45	3.51	3.25	17.76
0.0751	0.679	35	5.8	4.75	73.4164
0.127	0.39	8.53	3.98	5.75	0
0.127	0.39	8.53	3.98	1.75	0
0.127	0.39	8.53	3.98	4.75	0
0.127	0.39	8.53	3.98	2.75	0
0.127	0.39	8.53	3.98	4.25	0
0.127	0.39	8.53	3.98	5.25	0
0.127	0.39	8.53	3.98	2.25	0
0.127	0.39	8.53	3.98	3.25	0
0.127	0.39	8.53	3.98	3.75	0
0.127	0.39	8.53	3.98	1.25	0
0.127	0.39	8.53	3.98	6.25	0
0.122	0.8	21.6	5.14	3.25	41.08965

0.155	4.67	70	4.5	1.25	0
0.128671	1.22	39.83	8	1.25	0
0.077	0.047	18.23	7.8	1.75	20.13612
0.0031	0.05	9.83	2.39	0.75	0
0.0031	0.05	9.83	2.39	1.75	0
0.0751	0.679	35	5.8	3.75	26.9756
0.086	0.05	9.83	2.39	0.25	0
0.088	0.16	27.7	3.6	2.25	76.96
0.172	12.29	45	4.3	5.75	0
0.147	23.57	24	8.5	3.25	0
0.0599	1.92	45	5.8	2.75	1468.362
0.0859	2.358	45	3.51	2.75	216.9321
0.0166	0.39	49	2	1.25	814.8679
0.253	1.019	45	2.51	1.25	0
0.0869	21.8	45	3.5	1.25	0
0.0869	21.8	45	3.5	0.75	0
0.136	0.39	8.53	3.98	4.75	0
0.136	0.39	8.53	3.98	2.25	0
0.136	0.39	8.53	3.98	1.25	0
0.136	0.39	8.53	3.98	6.25	0
0.136	0.39	8.53	3.98	0.75	0
0.136	0.39	8.53	3.98	3.75	0
0.047	4.47	70	4.5	3.25	0
0.085	3.29	19.2	3.2	5.75	0
0.085	3.29	19.2	3.2	3.75	0
0.085	3.29	19.2	3.2	3.25	0
0.085	3.29	19.2	3.2	4.75	0
0.085	3.29	19.2	3.2	5.25	0
0.085	3.29	19.2	3.2	4.25	0
0.044	4.6	45	5.8	4.75	58.73312
0.043	36.56	45	4.43	1.75	65.28301
0.085	0.05	9.83	2.39	1.75	66.6
0.023	0.29	50	3.4	4.25	507.3351
0.085	0.05	9.83	2.39	2.75	0
0.0595	0.9	21.6	5.14	4.25	0
0.325	0.858	31.19	3.1	0.75	0
0.047	4.47	70	4.5	1.75	282.3814
0.154	6.3	45	4.43	0.75	0
0.154	6.3	45	4.43	3.75	0
0.088	1.8	45	3.51	4.75	0
0.079	3.2	45	5.8	3.75	155.3205
0.093	29.17	45	5.8	1.75	71.04
0.147	2.62	45	3.51	1.25	20.13612
0.154	6.3	45	4.43	1.25	0
0.154	6.3	45	4.43	2.25	0
0.097	14.54	45	4.3	2.25	708.0592
0.155	0.729	45	4.43	0.75	0
0.0599	1.92	45	5.8	4.25	722.2453
0.0414	1.92	45	5.8	5.25	0
0.043	1.2	45	4.43	4.25	2912.768
0.03	5.09	45	5.8	4.25	289.2007
0.0595	0.9	21.6	5.14	2.25	772.0653
0.171	5.7	21.7	4.2	1.25	0
0.171	5.7	21.7	4.2	2.25	0
0.147	23.57	24	8.5	0.75	0
0.0798	3.7	45	5.8	2.25	814.4979

0.3	0.39	8.53	3.98	5.25	0
0.3	0.39	8.53	3.98	2.75	0
0.3	0.39	8.53	3.98	1.75	0
0.3	0.39	8.53	3.98	6.25	0
0.026	0.39	49	2	3.75	0
0.326	0.636	18.23	7.8	0.25	0
0.326	0.636	18.23	7.8	1.25	0
0.0589	0.679	35	5.8	2.25	0
0.253	1.16	45	4.3	1.25	0
0.0599	1.92	45	5.8	3.25	903.0378
0.03	5.09	45	5.8	3.75	632.0703
0.044	4.6	45	5.8	4.25	22.22
0.102	3.29	19.2	3.2	5.25	0
0.102	3.29	19.2	3.2	3.75	0
0.102	3.29	19.2	3.2	6.25	0
0.102	3.29	19.2	3.2	4.25	0
0.102	3.29	19.2	3.2	4.75	0
0.102	3.29	19.2	3.2	5.75	0
0.206	0.219	27.7	3.6	2.25	0
0.122	0.8	21.6	5.14	1.75	167.9658
0.172	12.29	45	4.3	2.25	0
0.227	0.452	35	5.8	5.75	0
0.1957	0.085	14.6	2	3.75	0
0.1957	0.085	14.6	2	1.25	0
0.227	0.452	35	5.8	3.75	0
0.1957	0.085	14.6	2	2.25	0
0.1957	0.085	14.6	2	4.75	0
0.1957	0.085	14.6	2	5.75	0
0.042	4.3	45	5.8	3.25	1714.421
0.154	15.616	45	3.5	4.75	0
0.154	15.616	45	3.5	1.75	0
0.154	15.616	45	3.5	3.75	0
0.154	15.616	45	3.5	2.75	0
0.147	2.62	45	3.51	0.25	0
0.0798	3.7	45	5.8	2.75	1180.52
0.047	4.47	70	4.5	2.75	416.9666
0.149	0.085	14.6	2	5.75	0
0.227	0.452	35	5.8	2.75	0
0.227	0.452	35	5.8	1.75	0
0.0595	0.9	21.6	5.14	3.25	223.0629
0.023	0.29	50	3.4	3.25	224.3942
0.023	0.29	50	3.4	3.75	1251.077
0.136	0.39	8.53	3.98	3.25	0
0.136	0.39	8.53	3.98	5.75	0
0.136	0.39	8.53	3.98	1.75	0
0.136	0.39	8.53	3.98	5.25	0
0.136	0.39	8.53	3.98	2.75	0
0.035	8.3	45	5.8	5.25	722.2453
0.172	12.29	45	4.3	5.25	0
0.0414	1.92	45	5.8	4.25	44.44
0.052	4.3	45	5.8	5.25	0
0.044	4.6	45	5.8	5.25	0
0.147	2.62	45	3.51	2.75	708.8314
0.171	5.7	21.7	4.2	3.75	0
0.171	5.7	21.7	4.2	2.75	0
0.171	5.7	21.7	4.2	4.75	0

0.286	0.085	14.6	2	4.75	0
0.28	15.46	45	4.3	0.75	0
0.28	15.46	45	4.3	3.75	0
0.28	15.46	45	4.3	5.75	0
0.28	15.46	45	4.3	2.75	0
0.286	0.085	14.6	2	0.75	0
0.149	0.085	14.6	2	4.75	0
0.172	12.29	45	4.3	4.75	0
0.253	1.019	45	2.51	4.75	0
0.253	1.019	45	2.51	2.25	0
0.206	0.219	27.7	3.6	1.25	0
0.155	4.67	70	4.5	2.75	0
0.147	23.57	24	8.5	2.25	0
0.154	6.3	45	4.43	1.75	0
0.121	0.867	31.19	3.1	1.75	8.88
0.179	0.39	8.53	3.98	4.75	0
0.179604	0.39	8.53	3.98	0.75	0
0.179	0.39	8.53	3.98	5.75	0
0.179	0.39	8.53	3.98	5.25	0
0.179	0.39	8.53	3.98	2.25	0
0.179	0.39	8.53	3.98	1.75	0
0.179	0.39	8.53	3.98	3.25	0
0.179	0.39	8.53	3.98	3.75	0
0.043	36.56	45	4.43	3.75	0
0.149	0.085	14.6	2	2.25	0
0.149	0.085	14.6	2	1.25	0
0.0595	0.9	21.6	5.14	2.75	313.09
0.0595	0.9	21.6	5.14	3.75	0
0.197	0.679	35	5.8	4.75	0
0.197	0.679	35	5.8	5.75	0
0.197	0.679	35	5.8	2.75	0
0.197	0.679	35	5.8	3.75	0
0.3	0.39	8.53	3.98	4.75	0
0.047	4.47	70	4.5	2.25	368.1458
0.149	0.085	14.6	2	3.75	0
0.093	29.17	45	5.8	3.75	112.1258
0.172	12.29	45	4.3	1.25	0
0.198	0.39	8.53	3.98	1.25	0
0.198	0.39	8.53	3.98	3.75	0
0.198	0.39	8.53	3.98	2.75	0
0.198	0.39	8.53	3.98	5.25	0
0.149	0.085	14.6	2	2.75	0
0.147	2.62	45	3.51	1.75	599.5818
0.206	0.219	27.7	3.6	0.25	0
0.187	0.219	27.7	3.6	5.75	0
0.187	0.219	27.7	3.6	6.75	0
0.155	4.67	70	4.5	5.75	0
0.155	4.67	70	4.5	2.25	0
0.155	4.67	70	4.5	4.75	0
0.043	36.56	45	4.43	4.25	293.6656
0.206	0.219	27.7	3.6	1.75	0
0.1957	0.085	14.6	2	2.75	0
0.0414	1.92	45	5.8	3.25	525.7474
0.043	36.56	45	4.43	2.25	145.7272
0.149	0.085	14.6	2	1.75	0
0.206	0.219	27.7	3.6	0.75	0

0.154	6.3	45	4.43	3.25	0
0.326	0.636	18.23	7.8	2.25	0
0.155	4.67	70	4.5	1.75	53.95119
0.0233	4.02	23.66	2.8	3.75	0
0.093	0.827	39.83	8	3.75	0
0.058	1.22	39.83	8	4.75	188.616
0.206	0.219	27.7	3.6	2.75	0
0.204	0.022	18.23	7.8	6.75	0
0.204	0.022	18.23	7.8	3.25	0
0.206	0.865	24.39	6.5	3.25	0
0.206	0.865	24.39	6.5	0.25	0
0.206	0.865	24.39	6.5	6.25	0
0.206	0.865	24.39	6.5	7.75	0
0.206	0.865	24.39	6.5	1.25	0
0.206	0.865	24.39	6.5	4.25	0
0.206	0.865	24.39	6.5	5.25	0
0.206	0.865	24.39	6.5	2.25	0
0.088	1.8	45	3.51	1.75	16.68637
0.095	3.03	23.66	2.8	2.25	53.28
0.0859	2.358	45	3.51	3.75	0
0.198	0.39	8.53	3.98	4.25	0
0.198	0.39	8.53	3.98	2.25	0
0.198	0.39	8.53	3.98	5.75	0
0.206	0.865	24.39	6.5	0.75	0
0.2154	5.29	45	5.8	0.75	0
0.147	2.62	45	3.51	3.75	73.4164
0.253	1.16	45	4.3	3.25	0
0.043	1.2	45	4.43	3.25	1700.835
0.325	0.858	31.19	3.1	2.75	0
0.253	1.16	45	4.3	0.75	0
0.253	1.16	45	4.3	5.25	0
0.154	6.3	45	4.43	4.75	0
0.253	1.16	45	4.3	1.75	0
0.155	4.67	70	4.5	3.25	0
0.136	0.39	8.53	3.98	4.25	0
0.286	0.085	14.6	2	1.25	0
0.286	0.085	14.6	2	2.25	0
0.172	12.29	45	4.3	2.75	255.4632
0.204	0.022	18.23	7.8	4.75	0
0.204	0.022	18.23	7.8	5.75	0
0.147	2.62	45	3.51	2.25	125.2583
0.253	1.16	45	4.3	4.25	0
0.206	0.865	24.39	6.5	6.75	0
0.093	29.17	45	5.8	4.75	0
0.0599	1.92	45	5.8	4.75	0
0.209	0.085	14.6	2	4.25	0
0.209	0.085	14.6	2	6.75	0
0.209	0.085	14.6	2	5.25	0
0.088	1.8	45	3.51	2.25	106.56
0.206	0.865	24.39	6.5	4.75	0
0.206	0.865	24.39	6.5	5.75	0
0.206	0.865	24.39	6.5	1.75	0
0.206	0.865	24.39	6.5	3.75	0
0.206	0.865	24.39	6.5	2.75	0
0.171	5.7	21.7	4.2	1.75	0
0.0414	1.92	45	5.8	3.75	381.6037

0.198	0.39	8.53	3.98	4.75	0
0.198	0.39	8.53	3.98	1.75	0
0.3	0.39	8.53	3.98	1.25	0
0.198	0.39	8.53	3.98	0.75	0
0.198	0.39	8.53	3.98	3.25	0
0.0747	17.14	24	8.5	3.75	0
0.209	0.085	14.6	2	3.25	0
0.197	0.679	35	5.8	4.25	0
0.197	0.679	35	5.8	3.25	0
0.197	0.679	35	5.8	5.25	0
0.197	0.679	35	5.8	1.75	0
0.209	0.085	14.6	2	1.75	0
0.211418	0.085	14.6	2	0.75	0
0.227	0.452	35	5.8	4.75	0
0.0962	0.29	50	3.4	1.25	0
0.0962	0.29	50	3.4	3.75	0
0.0962	0.29	50	3.4	6.25	0
0.0962	0.29	50	3.4	8.25	0
0.0962	0.29	50	3.4	5.25	0
0.0962	0.29	50	3.4	4.75	0
0.0962	0.29	50	3.4	7.25	0
0.0962	0.29	50	3.4	2.75	0
0.043	1.2	45	4.43	2.25	1318.284
0.2154	5.29	45	5.8	1.75	0
0.308	0.116	18.23	7.8	2.75	0
0.204	0.022	18.23	7.8	2.75	0
0.1957	0.085	14.6	2	1.75	0
0.21	0.085	14.6	2	0.25	0
0.1957	0.085	14.6	2	4.25	0
0.1957	0.085	14.6	2	5.25	0
0.204	0.022	18.23	7.8	1.25	0
0.28	15.46	45	4.3	1.75	0
0.122	0.8	21.6	5.14	1.25	0
0.253	1.16	45	4.3	2.75	0
0.325	0.858	31.19	3.1	1.75	17.76
0.3	0.39	8.53	3.98	4.25	0
0.0159	0.729	45	2.51	2.25	574.321
0.042	4.3	45	5.8	7.25	0
0.122	0.8	21.6	5.14	2.25	0
0.0458	2.56	45	5.8	0.75	1157.029
0.204	0.022	18.23	7.8	3.75	0
0.28	15.46	45	4.3	4.75	0
0.0233	4.02	23.66	2.8	3.25	97.88853
0.227	0.452	35	5.8	3.25	0
0.308	0.116	18.23	7.8	0.75	0
0.204	0.022	18.23	7.8	2.25	0
0.043	1.2	45	4.43	3.75	620.6516
0.3	0.39	8.53	3.98	4.75	0
0.3	0.39	8.53	3.98	0.75	0
0.3	0.39	8.53	3.98	2.75	0
0.3	0.39	8.53	3.98	5.75	0
0.3	0.39	8.53	3.98	1.75	0
0.3	0.39	8.53	3.98	3.75	0
0.34	0.08	7.2	4.2	2.75	0
0.34	0.08	7.2	4.2	0.75	0
0.34	0.08	7.2	4.2	3.75	0

0.34	0.08	7.2	4.2	4.75	0
0.34	0.08	7.2	4.2	1.75	0
0.2154	5.29	45	5.8	0.25	0
0.154	6.3	45	4.43	6.25	0
0.035	8.3	45	5.8	6.25	0
0.0798	3.7	45	5.8	4.75	0
0.0962	0.29	50	3.4	2.25	0
0.308	0.116	18.23	7.8	7.75	0
0.308	0.116	18.23	7.8	5.25	0
0.326	0.263	27.7	3.6	2.75	0
0.147	2.62	45	3.51	3.25	0
0.286	0.085	14.6	2	3.75	0
0.286	0.085	14.6	2	1.75	0
0.3	0.39	8.53	3.98	3.75	0
0.3	0.39	8.53	3.98	3.25	0
0.095	3.03	23.66	2.8	3.25	0
0.088	1.8	45	3.51	3.75	0
0.325	0.858	31.19	3.1	0.25	0
0.0756	2.064	24.39	6.5	2.75	35.52
0.3	0.39	8.53	3.98	2.25	0
0.172	12.29	45	4.3	3.25	264.8312
0.187	0.219	27.7	3.6	4.25	0
0.058	1.22	39.83	8	5.25	684.9927
0.183	3.29	19.2	3.2	3.75	0
0.183	3.29	19.2	3.2	3.25	0
0.183	3.29	19.2	3.2	4.75	0
0.183	3.29	19.2	3.2	5.75	0
0.183	3.29	19.2	3.2	4.25	0
0.183	3.29	19.2	3.2	5.25	0
0.28	15.46	45	4.3	0.25	0
0.28	15.46	45	4.3	5.25	0
0.325	0.858	31.19	3.1	1.25	0
0.057	1.69	24.39	6.5	4.25	0
0.052	4.3	45	5.8	0.25	0
0.308	0.116	18.23	7.8	6.25	0
0.0962	0.29	50	3.4	3.25	0
0.0962	0.29	50	3.4	5.75	0
0.0962	0.29	50	3.4	4.25	0
0.0962	0.29	50	3.4	6.75	0
0.28	15.46	45	4.3	3.25	0
0.088	1.8	45	3.51	3.25	0
0.204	0.022	18.23	7.8	5.25	0
0.204	0.022	18.23	7.8	0.75	0
0.204	0.022	18.23	7.8	6.25	0
0.042	13.61	32.3	3	2.75	10.656
0.308	0.116	18.23	7.8	3.75	0
0.308	0.116	18.23	7.8	2.25	0
0.308	0.116	18.23	7.8	4.75	0
0.243	0.679	35	5.8	2.25	23.68
0.28	15.46	45	4.3	1.25	0
0.253	1.019	45	2.51	3.25	0
0.326	0.263	27.7	3.6	0.75	0
0.253	1.019	45	2.51	1.75	0
0.093	29.17	45	5.8	4.25	0
0.0798	3.7	45	5.8	4.25	0
0.187	0.219	27.7	3.6	2.75	0

0.187	0.219	27.7	3.6	6.25	0
0.326	0.263	27.7	3.6	1.25	0
0.286	0.085	14.6	2	2.75	0
0.227	0.452	35	5.8	1.25	0
0.326	0.263	27.7	3.6	1.75	0
0.172	12.29	45	4.3	3.75	0
0.043	1.2	45	4.43	5.75	0
0.057	1.69	24.39	6.5	3.75	0
0.286	0.085	14.6	2	0.25	0
0.326	0.263	27.7	3.6	2.25	0
0.308	0.116	18.23	7.8	1.75	0
0.043	1.2	45	4.43	4.75	0
0.0034	0.32	78	0.4	0.75	0
0.088	1.8	45	3.51	2.75	17.76
0.3	0.39	8.53	3.98	0.75	0
0.308	0.116	18.23	7.8	4.25	0
0.0798	3.7	45	5.8	3.75	0
0.0326	24.06	24	8.5	0.25	53.28
0.042	4.3	45	5.8	3.75	0
0.243	0.679	35	5.8	0.25	0
0.28	15.46	45	4.3	4.25	0
0.28	15.46	45	4.3	2.25	0
0.326	0.263	27.7	3.6	0.25	0
0.187	0.219	27.7	3.6	3.75	0
0.19	0.84	31.19	3.1	4.75	0
0.012	1.43	23.66	2.8	0.25	0
0.043	1.2	45	4.43	5.25	0
0.042	4.3	45	5.8	4.25	0
0.187	0.219	27.7	3.6	5.25	0
0.19	0.84	31.19	3.1	6.25	0
0.19	0.84	31.19	3.1	2.75	0
0.19	0.84	31.19	3.1	4.25	0
0.294	0.832	18.23	7.8	7.75	0
0.294	0.832	18.23	7.8	3.25	0
0.294	0.832	18.23	7.8	1.25	0
0.032	14.716	45	2.51	0.25	0
0.308	0.116	18.23	7.8	6.75	0
0.19	0.84	31.19	3.1	0.75	0
0.19	0.84	31.19	3.1	3.25	0
0.19	0.84	31.19	3.1	3.75	0
0.19	0.84	31.19	3.1	1.75	0
0.19	0.84	31.19	3.1	5.75	0
0.294	0.832	18.23	7.8	5.75	0
0.155	0.729	45	4.43	0.25	0
0.3	0.39	8.53	3.98	4.25	0
0.3	0.39	8.53	3.98	2.25	0
0.19	0.84	31.19	3.1	5.25	0
0.187	0.219	27.7	3.6	1.75	0
0.294	0.832	18.23	7.8	2.75	0
0.629	0.9	21.6	5.14	4.25	0
0.629	0.9	21.6	5.14	1.75	0
0.05	0.29	50	3.4	2.25	17.76
0.294	0.832	18.23	7.8	6.75	0
0.294	0.832	18.23	7.8	3.75	0
0.294	0.832	18.23	7.8	0.25	0
0.389	30.89	24	8.5	6.25	311.08

0.389	30.89	24	8.5	0.75	0
0.294	0.832	18.23	7.8	0.75	0
0.294	0.832	18.23	7.8	4.75	0