

An Empirical Method for Characterizing Standing Crops of Aquatic Vegetation¹

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ABSTRACT

Data from 55 Florida lakes were used to demonstrate that the maximum measured standing crop of emergent, floating-leaved, and submersed plants can be used to provide a simple characterization of macrophyte standing crops in the littoral zones of lakes. The maximum standing crop was strongly related to the mean standing crop of emergent ($R^2 = 0.83$), floating-leaved ($R^2 = 0.64$), and submersed ($R^2 = 0.85$) macrophytes, and there was also a strong relationship ($R^2 = 0.79$) when data from all plant types were combined. Our best-fit regression equations were $\ln EB = 1.07 \ln MEB - 1.19$, $\ln FB = 1.28 \ln MFB - 2.73$, $\ln SB = 1.20 \ln MSB - 1.98$, and $\ln TMB = 1.20 \ln MTMB - 2.11$ where EB, FB, SB, and TMB are the average standing crops (g dry wt m⁻²) of emergent, floating-leaved, submersed, and total macrophytes respectively, and MEB, MFB, MSB, and MTMB are the maximum standing crops measured for the different groups. Standard errors of estimates for the average standing crops of the different plant types in individual lakes were of similar magnitude to the errors of estimates obtained for the mean-maximum standing crop regression equations. These analyses suggest that the maximum standing crop of aquatic macrophytes can provide useful information to characterize macrophyte standing crop in the littoral zone of lakes.

Key words: aquatic plants, biomass, lakes, models, littoral, limnology

INTRODUCTION

The overall goal of many aquatic vegetation sampling studies is to obtain an estimate of mean macrophyte stand-

ing crop. Standard sampling theory (APHA 1985) indicates that the number of samples necessary to characterize macrophyte standing crop using a random sampling design can be calculated from,

$$N = [(t \times S)/(d \times X)]^2$$

where N = number of sampling stations; t = Student's t at a given probability level; S = standard deviation, X = estimated true population mean; d = permissible error of the final mean. Thus, the number of sampling stations necessary to characterize the mean macrophyte standing crop changes proportionally to the square of the coefficient of variation and to the inverse of the square of the permissible error (Figure 1). Because the coefficient of variation associated with the mean macrophyte standing crop is often > 50 %, the number of sampling stations necessary to estimate the mean macrophyte standing crop, especially with a permissible error of 10 % as is often re-

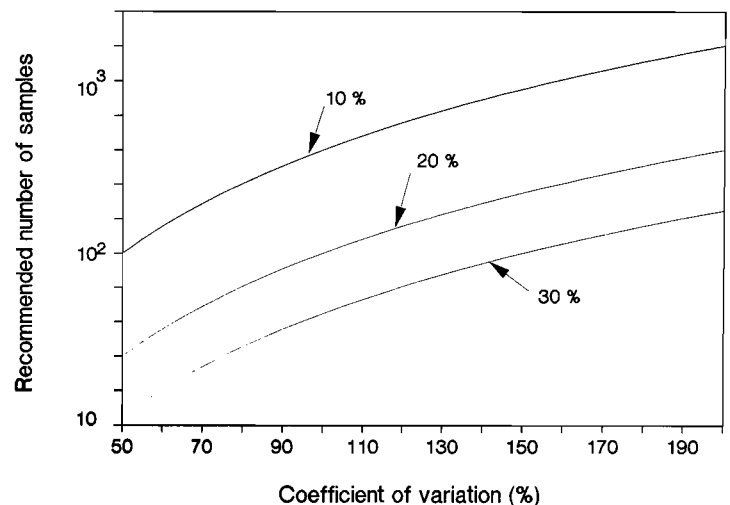


Figure 1. The relationship between the variability of the mean (as the coefficient of variation) and the number of samples necessary to estimate the mean with a permissible error of 10, 20, and 30% (from APHA 1985).

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commended (e.g., APHA 1985), is typically > 200 (Figure 1). A large number of samples is still needed even if more conservative sampling (permissible error > 10 %) or stratified random sampling programs are adopted. For instance, Nichols (1982) concluded that if a stratified random design was used over 100 samples would be needed to adequately estimate the aquatic macrophyte standing crop in Lilly Lake, a small (37 ha) hard-water lake in Wisconsin.

Lake surveys have been used to identify large-scale limnological patterns in lakes (cf. Peters 1986). Although the average precision of lake survey data is low because of limited (3 to 4 samples) sampling on individual lakes (e.g., Knowlton et al. 1984), data from these surveys have been used successfully to develop simple empirical models that assess the relationships between environmental factors and organismal abundance (cf. Peters 1986). These simple models have found wide spread use in lake management (Peters 1986), but only a few empirical models have been proposed to describe relationships between aquatic macrophytes and other organisms or to predict the abundance of aquatic macrophytes in lakes (e.g., Canfield et al. 1984; Durocher et al. 1984; Duarte et al. 1986; Canfield and Duarte 1988).

We believe the limited development of empirical macrophyte models is a direct consequence of the constraints (e.g., costs) imposed by the large number of samples required to statistically characterize macrophyte abundance in lakes (e.g., Nichols 1982; Downing and Anderson 1985). Large-scale limnological studies of aquatic macrophytes and the development of empirical models would be encouraged if macrophyte abundance in lakes could be characterized by the use of fewer samples. Here, we discuss the use of maximum measured macrophyte standing crop as a possible measure for characterizing macrophyte abundance within lakes.

METHODS

Data used in this study were primarily taken from an unpublished study (Canfield and Joyce 1985) of the macrophyte communities of 55 lakes located in Florida's Ocala National Forest (Latitude 29° 15' S, Longitude 81° 45' W). These lakes are generally small (area range 1 to 722 ha), shallow (mean depth < 6 m), and acidic (mean pH = 5.0), but they differ greatly in water transparency (range 0.3 to 5.8 m) and nutrient concentrations (total phosphorus range 6 to 142 mg m⁻³; cf. Greis 1985). The macrophyte communities were sampled between July and September of 1985. Using existing bathymetric maps (Greis 1985), 10 sampling transects were uniformly located around the perimeter of each lake prior to visiting the lake. At the lake, sampling stations were randomly established in the emergent, floating leaved, and submersed plant zones (30 stations per lake). All above-ground plant standing crop within a 0.25 m² quadrat were collected at each station. Sampled plants were placed in nylon mesh bags and spun to remove excess water. Samples were then weighed to the nearest 0.10 kg fresh weight.

Additional data were also obtained from the published literature (e.g., Adams and McCracken 1974; Wile 1974; Duarte 1987a). To compare data from the Florida lakes

with values reported elsewhere, which are generally expressed as g dry weight per m², plant water content was assumed to be 90% of the fresh weight (Westlake 1965). Relationships between the mean and the maximum standing crop for each plant type (emergent, floating leaved, and submersed) and for the macrophytes as a group were established by least squares regression analyses, following logarithmic transformation of the independent and dependent variables to meet the assumptions of least squares regression analysis. For our purposes here, maximum standing crop refers only to the largest standing crop measured during the sampling period.

RESULTS AND DISCUSSION

Relationships between mean and maximum macrophyte standing crop. Average emergent standing crops in the Ocala National Forest lakes ranged from 22 to 720 g dry wt./m² with a median value of 342 g dry wt./m². Average floating-leaved standing crops ranged from 0 to 876 (median = 120) g dry wt./m² and mean submersed standing crops ranged from 0 to 510 (median = 112) g dry wt./m². There, however, were strong relationships between the measured mean and maximum standing crops for the three major aquatic macrophyte (emergent, floating-leaved, and submersed) types (Table 1; Figure 2). Further, the relationships between the maximum and mean macrophyte standing crop were very similar for the different plant types (Figure 2a-c) and there also was a strong relationship ($R^2 = 0.79$) between the measured mean and maximum standing crop when all plant types were combined (Eq. 4, Table 1; Figure 2d). Only the equation for floating-leaved standing crop (Eq. 2) was statistically (t-test, $p < 0.05$) different from the equations describing the relationship between the mean and maximum standing crop for emergent and submersed macrophytes (Eq. 1 and 3; Table 1).

The within-lake standing crop variability was considerable for the macrophyte communities in the Ocala National Forest lakes. Average coefficients of variation (CV) for the individual lake-average standing crop of emergent, floating-leaved, and submersed macrophytes were 60%, 120%, and 86%, respectively. The large errors associated with the estimation of the mean macrophyte standing crop of emergent, floating-leaved, and submersed macrophyte standing crop in the individual lakes, however, were of similar magnitude to the errors of the relationship between the maximum and mean macrophyte standing crop (Eqs. 1-4,

TABLE 1. REGRESSION COEFFICIENTS FOR MODELS ESTIMATING AVERAGE MACROPHYTE STANDING CROP (Ab) FROM THE MAXIMUM STANDING CROP (Mb) IN g DRY WT. M⁻². THE COEFFICIENTS CORRESPOND TO THE MODEL: $\ln Ab = a + b * \ln Mb$. THE TABLE ALSO SHOWS THE COEFFICIENT OF DETERMINATION (R^2) AND STANDARD ERROR OF THE TRANSFORMED ESTIMATES (S.E._{ln est}) AS AN INDICATION OF FIT. $P < 0.0001$ FOR ALL EQUATIONS.

| Macrophytes | a | b | R ² | S.E. _{ln est} | Eq. |
|-----------------|-------|------|----------------|------------------------|-----|
| Emergent | -1.19 | 1.07 | 0.83 | 0.26 | (1) |
| Floating-leaved | -2.73 | 1.28 | 0.64 | 0.52 | (2) |
| Submersed | -1.98 | 1.20 | 0.85 | 0.42 | (3) |
| All Plant Types | -2.11 | 1.20 | 0.79 | 0.43 | (4) |

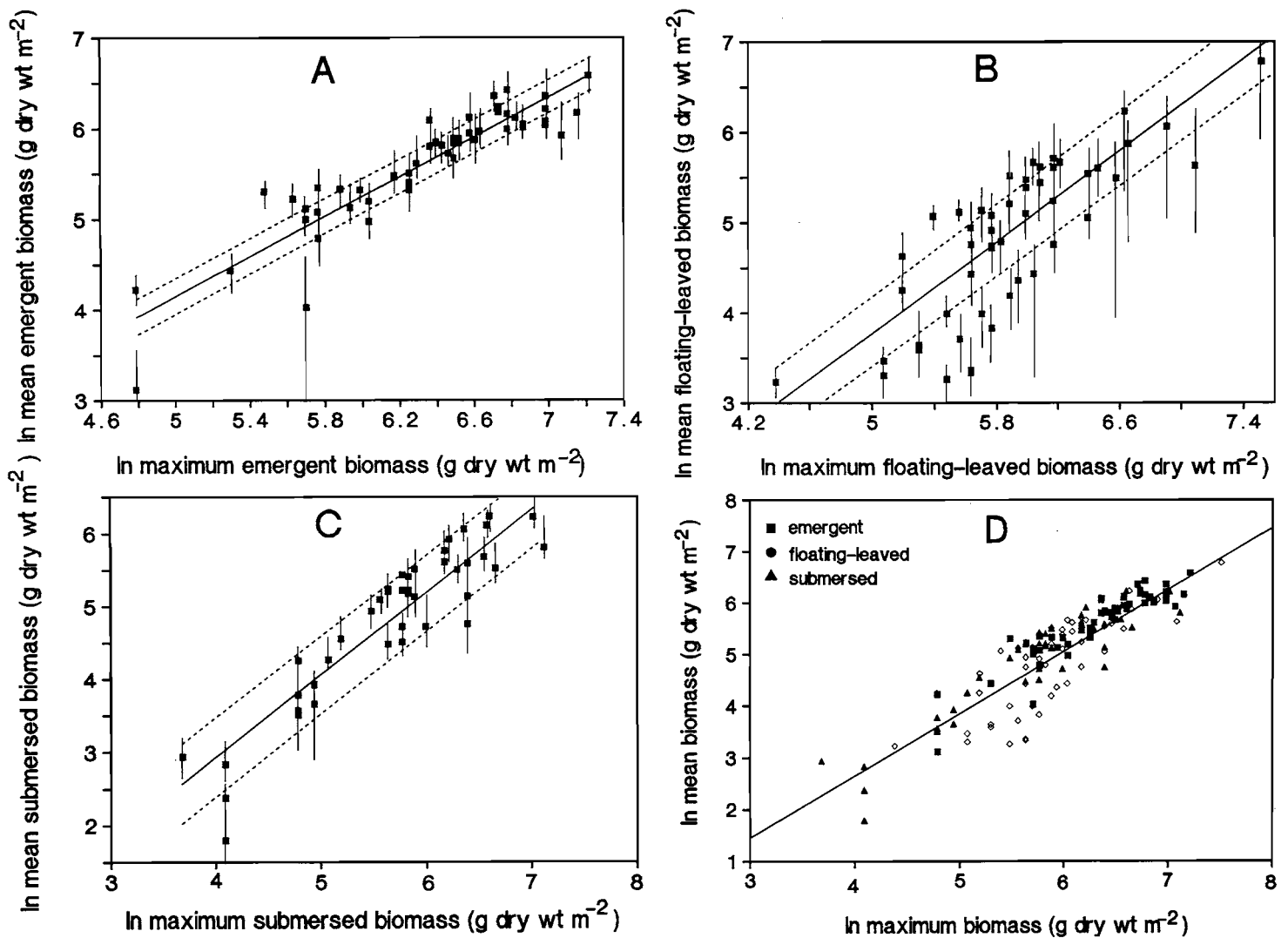


Figure 2. The relationship between the maximum and mean standing crop of (a) emergent, (b) floating-leaved, (c) submersed macrophytes, and (d) all groups combined. The lines correspond to the regression equations in Table 2. Vertical bars are \pm one standard error.

Table 1; Figure 2a-c). This suggested that little additional information about the mean standing crop was gained by placing more effort in sampling than that necessary to estimate the maximum plant standing crop in the lake.

Our data base consisted of lakes located in a limited geographic area, the Ocala National Forest of Florida. Because the limnological characteristics of these lakes are not typical of lakes elsewhere, we tested the generality of Eqs. 3 and 4 by comparing our results with independent data derived from aquatic systems located throughout the world (Table 2). We tested only Eqs. 3 and 4 because studies that provide the required information for emergent and floating-leaved macrophytes are rare. Although the studies from the published literature differed greatly in sampling design and intensity, both Eqs. 3 and 4 produced unbiased estimates (slope = 1, $P > 0.5$; intercept = 0, $P > 0.5$) of average submersed standing crop from the recorded maximum standing crop (Figure 3), and both equations were equally precise (S.E. In estimate from Eq. 3 = 0.51, S.E. In estimate from Eq. 4 = 0.52). Only 11 of the 25 published studies provided enough information to calcu-

late the error around the estimated average submersed standing crop. The magnitude of these errors, however, was comparable to the standard error for the predicted values (Eqs. 3 and 4, Table 1; Figure 3). These results confirm the generality of the relationship between maximum and mean standing crop, and further suggest that this relationship may be applicable to other aquatic ecosystems besides lakes for the literature data included 2 coastal ecosystems (Table 2).

Estimating macrophyte standing crop in lakes. A normal distribution of macrophyte standing crop within lakes is often assumed when plant sampling programs are initiated (APHA 1985). This assumption, however, is often violated because of the patchiness and skewed distribution of plant standing crops. For example, the distribution of submersed macrophyte standing crop in four northern lakes sampled intensively ($N > 200$; Duarte 1987a) shows strong (1.2 to 4.1) skewness (Figure 4). Strong skewness in the distribution of any population causes average values obtained from random sampling to provide a biased estimate of the central tendency of the distribution (Snedecor and

TABLE 2. MEAN AND MAXIMUM STANDING CROP (g DRY WEIGHT PER m²) OF SUBMERSED MACROPHYTES REPORTED IN 22 LAKES AND 2 COASTAL SYSTEMS.

| Lake | Mean | S.E. | N | Maximum | Reference |
|----------------------------|------|------|-----|---------|----------------------------------|
| Par pond | 214 | 128 | 12 | 423 | Grace and Tilley (1976) |
| Swartvlei | 914 | | | 1950 | Howard-Williams & Liptrot (1980) |
| St. Clair | 137 | 106 | 14 | 427 | Schloesser <i>et al.</i> (1985) |
| Warniak | 130 | | | 278 | Bernatowicz (1969) |
| Opinicon | 335 | | | 1559 | Crowder <i>et al.</i> (1977) |
| Mirror | 7.1 | | | 100 | Moeller (1985) |
| Wingra | 253 | | | 400 | Adams & McCracken (1974) |
| Mondarra | 1459 | 1484 | 20 | 6410 | Finlayson <i>et al.</i> (1984) |
| Stemsfjord | 333 | | | 750 | Roslett <i>et al.</i> (1984) |
| Halverson | 196 | | | 390 | Engel (1985) |
| Memphremagog | 57 | 60 | 44 | 212 | Duarte (Unpub. results) |
| d'Endine | 202 | 298 | 23 | 991 | Guilayson & Sarraceni (1974) |
| Simcoe | 67 | 100 | 51 | 586 | Neil & Kamaitis (1985) |
| Lunzer Untersee | 256 | 218 | 20 | 814 | Schlott & Malicky (1984) |
| Lunzer Untersee | 310 | 229 | 17 | 778 | " |
| Cocburn Sound ¹ | 470 | 230 | 21 | 1300 | Cambridge & McComb (1984) |
| Delta Marsh | 120 | 78 | 18 | 250 | Anderson (1978) |
| Biwa | 336 | | | 1000 | Ikusima (1984) |
| Stechlin | 450 | | | 1000 | Krausch (1985) |
| Pigeon | 237 | | | 470 | Wile (1974) |
| Chemung | 260 | | | 663 | " |
| Rice | 193 | | | 408 | " |
| Clear and Stony | 30 | | | 162 | " |
| Ninigret ¹ | 645 | 569 | 150 | 1584 | Thorne-Miller and Harlin (1984) |

¹Coastal ecosystems.

Cochran 1979). Consequently, plant sampling programs such as those proposed by Nichols (1982) or Downing and Anderson (1985) should be used whenever possible to obtain accurate estimates of mean standing crop.

The prospect of collecting a large number of plant samples (e.g., Nichols 1982) along with the associated costs in time and personnel has discouraged many scientists from characterizing macrophyte standing crop in their study

lakes whenever the primary focus of their study was not aquatic vegetation. The strong skewness of macrophyte standing crop distributions (e.g., Figure 4), however, has important implications for the characterization of macrophyte standing crop in lakes because it implies that failure to sample the most dense macrophyte stands will result in a biased estimate of the mean standing crop. The maximum macrophyte standing crop also not only constrains the average value, but it is statistically related to the standard error of the mean (see Snedecor and Cochran 1979). In addition, the maximum standing crop is an important characteristic of aquatic macrophyte populations

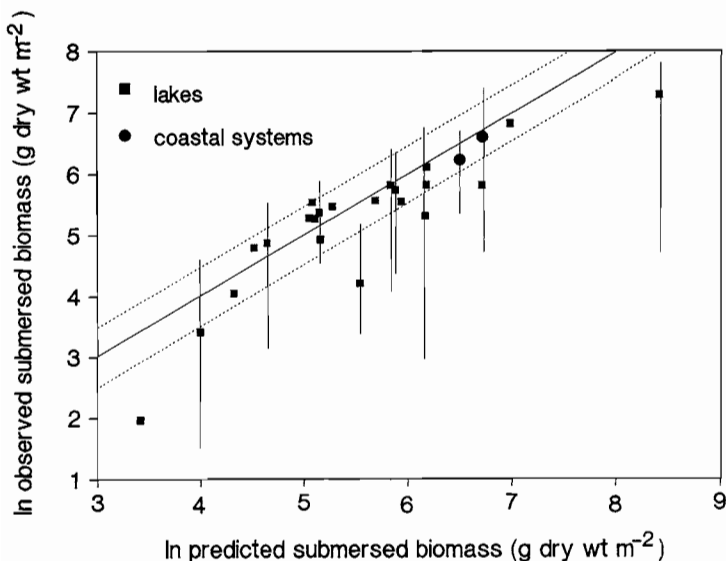


Figure 3. The relationship between the lake-average standing crop of submerged macrophytes and the values predicted from Eq. 4 (solid line). Vertical bars are + one standard error around the mean estimate, and broken lines represent the 95% confidence limits for Eq. 4 (Table 2). Equation 3 not shown because it is not significantly different ($P > 0.05$) from Eq. 4 (Table 1).

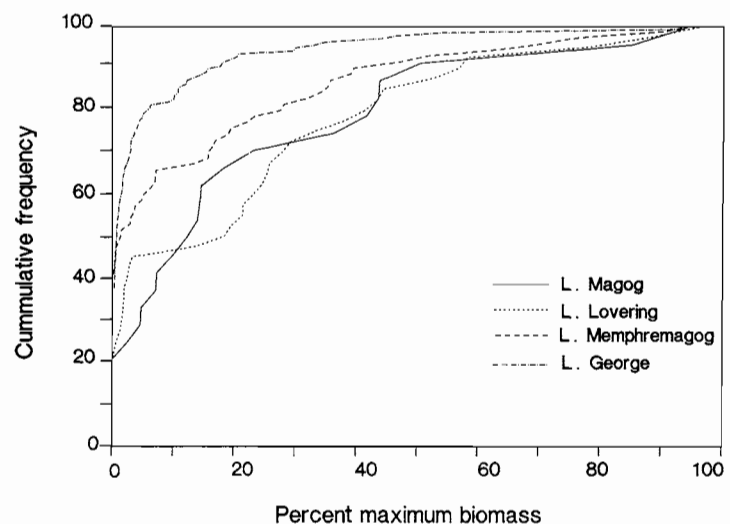


Figure 4. Cumulative frequency distributions for the standing crops of submerged macrophytes in four northern lakes ($N > 200$; data from Duarte 1987a).

because it represents the limit to macrophyte standing crop achieved within the lake and therefore provides information on the potential of the lake for macrophyte development.

To overcome the constraints imposed by traditional intensive sampling strategies (e.g., APHA 1985), we suggest that individuals interested in characterizing the standing crop of macrophytes in lakes for either comparative or descriptive purposes use a limited sampling program such as that described in this paper and the measured maximum standing crop of the different groups of macrophytes as their state variable when time or budget constraints make it difficult to accurately estimate the mean standing crop. We further suggest that the maximum measured macrophyte standing crops in a lake be used as a simple descriptor of macrophyte standing crop because (1) it sets the range of macrophyte standing crop for the lake studied, (2) it provides information on the potential of the lake for macrophyte development, (3) it is strongly related to the mean standing crop value (Figure 2 and 3), and (4) the identification of the maximum macrophyte standing stock in the lake is an important requirement to obtain reliable estimates of the mean no matter what type of sampling program is used (see Snedecor and Cochran 1979). Further, the regression equations we have provided (Table 1) seem to be sufficiently robust as to allow their use to estimate what the average standing crop in the lake may be from the maximum standing crop recorded, especially if the results are combined with fathometer techniques that have also been used to predict submersed plant standing crop (Maceina *et al.* 1984; Duarte 1987b).

Finding the maximum aquatic macrophyte standing crop in a lake is not difficult. The location where the maximum standing crop of emergent or floating-leaved macrophytes occurs can generally be found easily by visual surveys of the lake shoreline. The location where the maximum standing crop of submersed macrophytes occurs is more difficult to find, but can be found relatively easily by using (1) existing models that predict the depth where the maximum standing crop of submersed plants occurs (Chambers and Kalff 1985, Duarte and Kalff 1987), and (2) bathymetric charts to locate the areas where the littoral slope is most gentle (Duarte and Kalff 1986). Further, the maximum standing crop often corresponds to the tallest vegetation (Duarte 1987b), thus recording fathometers are particularly useful in finding this vegetation in large lakes. Although there is no simple way of assessing how far the estimated maximum standing crop may be from the true maximum standing crop in the lake, application of our regression equations to lakes for which detailed macrophyte data were available (i.e., L. Magog, L. Lovering, L. Memphremagog, L. George; data from Duarte 1987a) showed that the mean standing crop predicted from our regression equations (Eqs. 3 and 4; Table 1) was within the 95% confidence limits of the observed mean biomass whenever the estimated maximum biomass was within 50 to 70 % of the observed maximum biomass. This suggests that our estimation procedure is not extremely sensitive to inaccurate estimates of the maximum plant standing crop.

Accurate estimation of the mean standing crop of aquatic macrophytes in lakes is difficult. We, however, believe

that the use of the simple procedures described here will encourage future standing crop determinations of aquatic macrophytes in lakes and therefore begin to provide the badly needed data base that will permit large-scale limnological studies of aquatic macrophytes and the development of empirical macrophyte models. Our approach, however, should be considered a tentative method. Additional studies are needed on a broader range of lakes elsewhere to confirm the empirical relationships described in this paper.

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