

The Role of Aquatic Macrophytes in the Trophic Status of Northwestern Ontario Lakes

by

Terry R. Marshall©

A thesis submitted in partial fulfilment
of the requirements for the degree of
Master of Science in Biology

Department of Biology
Lakehead University
Thunder Bay, Ontario

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Abstract

This research focusses on the development, refinement, and assessment of regional trophic status models for lakes of northwestern Ontario. Two companion papers describe the application of image analysis of aerial photographs as a technique for mapping aquatic plant distribution, and the design of an innovative sampling device to simplify the collection of macrophytes.

Trophic status models were developed for lakes of northwestern Ontario, based on empirical relationships between Secchi disk transparency, total phosphorus, and chlorophyll *a* concentration. Corrective terms were added to the equations to adjust for the effect of water colour on Secchi disk transparency, and the effect of aquatic macrophyte abundance on the chlorophyll - phosphorus relationship. The adjusted models demonstrated an improvement in performance, as measured using standing stock of benthos as a response variable. These models would be expected to have applicability across the Precambrian Shield region of Canada.

Distributional maps of aquatic vegetation were produced for area lakes using digital image analysis of aerial photographs. Recent improvements in the price and performance of computer hardware and software make this a viable alternative to the conventional, visual mapping technique. The maps produced are highly detailed, with differentiation to species possible in some instances. Certain species may be further partitioned into density classes. The authenticity of the maps depends on the ability to properly define the spectral 'signatures' for different macrophyte types. These signatures were most easily defined for floating-leafed and emergent forms; submersed vegetation proved more difficult to classify. The main detriment to this approach is the steep learning curve associated with the image analysis software. A thorough description and

assessment of this technique is provided, with a discussion of its merits and deficiencies when compared with the conventional visual interpretive method.

A portable macrophyte sampler was designed for use in the relatively inaccessible lakes of this region. As such, it was required to be lightweight, easily transportable, and useable by a single person. The device is effective for obtaining quantifiable biomass samples of most rooted aquatic plants over a wide variety of substrates and sampling depths. Details on the design, operation, and performance of the sampler are documented within.

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I would like to express my gratitude to Dr. Peter Lee, who functioned as my supervisor and provided valued guidance throughout this endeavor. I also thank members of my graduate committee, Dr. Robert Rempel and Dr. Azim Mallik, and my external examiner, Dr. Alison Fox, for thorough and constructive reviews of the manuscript. Finally, I wish to thank Richard A. Ryder for his encouragement, support, and advice at all stages of the project.

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General Introduction

The trophic status of aquatic ecosystems is a measure of great importance to the resource manager. Lakes are commonly classified on this basis as a means of identifying their inherent productivity, and determining the degree to which this value may change due to future watershed development or lake restoration (Vollenweider 1968; Porcella et al. 1979). A suite of indices have been developed to evaluate lake trophic status (Shapiro 1977), with perhaps the best known being the Trophic State Index (TSI) of Carlson (1977).

Carlson's TSI models employ three indices of primary productivity - total phosphorus concentration, chlorophyll *a* concentration, and Secchi disk depth - either of which can be used to estimate lake trophic status. The models were developed using predictive equations which described the interrelationships among the primary productivity indices, as determined empirically from data from a continental lake set. The interrelationships can vary regionally, however, and Carlson's original equations have at times been modified to account for these differences (e.g. Aizaki et al. 1981; Osgood 1982). These modifications would have greatest utility when the TSI was applied over a fairly homogeneous area, such as the Precambrian Shield region of northwestern Ontario and northern Canada. Lakes of this region range from near colourless to highly dystrophic, so a further adjustment to account for the influence of water colour on Secchi disk transparency may be warranted. Aquatic macrophytes are also known to influence the production variables through a complex of interactions. As a final corrective, then, adjustments may be made to the TSI models to account for macrophyte biomass and cover. The first section of this thesis documents the development of TSI models for lakes of northwestern Ontario, with corrective terms included to account for differences in water colour and macrophyte abundance.

The performance of the various models is evaluated using the standing stock of benthos as a response variable.

To develop these models, it was necessary to determine macrophyte distribution and biomass from a number of test lakes. To accomplish this, a novel approach was adopted to produce maps of vegetation cover, as is described in the second section of the thesis. The distribution of macrophytes in many lakes is quite contagious, with the greatest concentrations occurring in shallow, nearshore zones. In such circumstances, the most efficient way to estimate macrophyte biomass is to first map their distribution across the lake surface, then sample randomly within representative plant beds. While these beds can be mapped from aerial photographs using the conventional, visual interpretative method, this is a very time-consuming process. In addition, the limited accuracy and precision of such maps may result in substantial errors when used to estimate plant biomass and production. To counter these concerns, vegetation maps were instead produced using an experimental, computer-aided approach, employing digital image analysis of aerial photographs. A thorough description of this automated mapping technique is provided, and its advantages and limitations are discussed.

The final section of the thesis describes a newly designed sampler for aquatic macrophytes. Due to the relative remoteness and inaccessibility of many lakes of northwestern Ontario, it was necessary to develop a lightweight sampling device which could be readily transported and operated by a single person. It was also important that this be a truly quantitative device, capable of deployment over a wide variety of water depths and substrates. The design and operation of this sampler is documented, and an assessment made of its effectiveness in collecting different types of plants on an assortment of substrates.

1. Trophic state models for lakes of northwestern Ontario, with corrections for water colour and aquatic macrophyte abundance

1.1 Abstract

The relationships between Secchi disk transparency, total phosphorus, and chlorophyll *a* concentration were examined for lakes of northwestern Ontario. These differ substantially from those reported for many continental and global lake sets, with less chlorophyll *a* and more light attenuation per unit of phosphorus. Trophic State Index (TSI) equations of Carlson (1977) were modified to reflect these differences, which would allow their application across lakes of the Laurentian Precambrian Shield. Water colour greatly influenced Secchi disk depth in these lakes, and a corrective term was added to the equations to account for this. The abundance of aquatic macrophytes explained a significant amount of the variance in the chlorophyll - phosphorus relationship. The addition of a macrophyte term, in addition to water colour, also improved the Secchi depth - chlorophyll *a* relationship. The superior performance of these TSI models was confirmed using total standing stock of benthos as a response variable.

1.2 Introduction

Numerous indices have been proposed to evaluate the trophic status of aquatic ecosystems (for a review, see Shapiro 1977; Porcella et al. 1979). While these indices vary considerably in complexity and utility, they share a common conceptual basis, and function by evaluating the availability of nutrients to a waterbody. They may do this directly (e.g. Vollenweider 1968; Dillon and Rigler 1974), or indirectly, by assessing the subsequent biological response to the nutrient

load, such as the depletion of dissolved oxygen (e.g. Hutchinson 1938; Lasenby 1975), or the accumulation of floral and faunal biomass or the composition of their respective species assemblages (e.g. Jarnefelt 1952; Brook 1965).

In popular use today is the Trophic State Index (TSI), developed by Carlson (1977) from a lake set representing continental North America. This model defines a trophic continuum along a scale ranging from 0 to 100, with each major division (i.e. unit of 10) representing a halving of water transparency and a doubling of algal biomass. TSI equations were developed using regression analysis which related Secchi disk transparency to chlorophyll *a* concentration or total phosphorus concentration. Each of these three input parameters represents a measure of primary productivity, and trophic status could be estimated for any lake or reservoir by utilizing any one parameter.

Problems may be encountered when applying a global or continental model, such as the TSI, for the assessment of a regional set of lakes. The contrast between values for the input variables is often quite low, compared to the breadth of data from which the model is based. Within this relatively narrow span of regional data, relationships among input parameters may be modified considerably by other processes which have little overall effect on a global scale (Aizaki et al. 1981; Hern et al. 1981; Osgood 1982). In these instances, it would be necessary to recalibrate the TSI model prior to its use, by replacing the original predictive equations between Secchi transparency, chlorophyll, and phosphorus with equations derived empirically from the regional data.

Water transparency is governed by its colour, along with inorganic and organic (i.e. algal) turbidity (Tyler 1968; Brezonik 1978). As such, water colour may modify the relationships between the TSI input variables, especially when these are calculated from lakes varying substantially in their

degree of staining. In such cases, a colour correction term would be expected to improve the performance of the models.

The relative abundance of aquatic macrophytes represents a second variable suspected to modify the relationships between the variables (Canfield 1983). Lakes with an abundance of macrophytes may experience reduced chlorophyll concentrations (e.g. Jones 1990), most likely due to a channelling of nutrients otherwise available to phytoplankton into both macrophytes and the epiphytes associated with them (Sand-Jensen and Sondergaard 1981; Canfield et al. 1983). Other processes may contribute to this phenomenon, such as the reduction of subsurface light levels due to dense macrophyte canopies (Titus and Adams 1979; Carter and Rybicki 1990), the production of allelopathic substances by macrophytes which may suppress phytoplankton growth (Crawford 1979; Wium-Andersen et al. 1982), and high zooplankton grazing rates associated with macrophyte dominated lakes (Timms and Moss 1984). With the exception of the Lake Evaluation Index of Porcella et al. (1979) and the water column phosphorus model of Canfield et al. (1983), no attempt has been made to incorporate macrophytes into a trophic state evaluator.

The purpose of this paper is to develop regional trophic state classification models, through the refinement of the original TSI equations of Carlson (1977). These were designed to characterize the productivity of lakes of northwestern Ontario, and by extension, other lakes of the Laurentian Precambrian Shield region of Canada. The degree to which further improvements can be made to these models, by consideration of water colour and aquatic plant biomass and cover, is examined. The total biomass of benthic fauna is used as a performance measure by which to test the relative efficiency of the refined models.

1.3 Methods

A set of 19 lakes located near Thunder Bay in northwestern Ontario was selected to encompass a wide range of water depth, nutrient concentration, water transparency, and macrophyte abundance (Table 1.1). Values for these and other measured parameters suggest that these lakes are broadly representative of small lakes of the Laurentian Precambrian Shield (Fee et al. 1989).

Standard limnological methods were used to determine lake area (AREA), mean depth (Z_{MEAN}), and maximum depth (Z_{MAX}). Samples were collected at various times during midsummer for estimation of water colour (COL), turbidity (TURB), and dissolved organic carbon (DOC), using the analytical methods described by the Ontario Ministry of the Environment (1981). Total phosphorus (TP) was determined from surface waters at spring overturn, sampled over a minimum of three years, and analyzed through the autoclave digestion method of Jeffries et al. (1977). Chlorophyll *a* (CHL), including pheophytin, was sampled repeatedly during midsummer, with samples integrated throughout the euphotic zone (defined as twice the Secchi depth), and analyzed spectrophotometrically. Secchi disk transparency (SD) was measured on numerous occasions during the midsummer period using a standard 20 cm diameter disk. Four lakes were of insufficient depth for the determination of Secchi depth, and this parameter was instead estimated by applying the regression equation established from the remaining lakes as

$$1) \quad \text{SD} = 7.37 - 2.22 * \log(\text{COL}) - 4.15 * \log(\text{TURB}) \quad (R^2 = 0.94; n = 15).$$

A stratified random design was adopted to determine macrophyte biomass. Plant zonation was established through visual interpretation and digital image analysis of colour infrared and true colour aerial photographs (see Section 2, this thesis). Plants were initially classed into groups

Table 1.1: Description of measured variables and their means and ranges. Littoral area refers to the lake area within the 5 m depth contour. Euphotic area refers to the lake area within the 2X Secchi depth contour.

Variable	Description	Units	Mean	Range
AREA	Lake area	ha	38	8 - 211
Z _{MEAN}	Mean depth	m	2.9	0.8 - 7.7
Z _{MAX}	Maximum depth	m	7.5	0.8 - 24.1
%LITT	% of lake area < 5.0 m deep	%	82	39 - 100
SD	Secchi disk transparency	m	3.0	0.9 - 6.7
DOC	Dissolved organic carbon	mg·L ⁻¹	10.2	3.8 - 17.3
COLOR	Water colour	Pt·L ⁻¹	43	5 - 100
TURB	Turbidity	JTU	1.8	0.8 - 3.3
TP	Total spring phosphorus	μg·L ⁻¹	13.3	7.0 - 20.7
CHL	Chlorophyll <i>a</i>	μg·L ⁻¹	2.9	0.6 - 5.7
PLNT _{ALL}	Total plant biomass per lake area	g·m ⁻²	4.6	0.2 - 16.6
PLNT _{LIT}	Total plant biomass per littoral area	g·m ⁻²	5.1	0.2 - 16.6
PLNT _{SUBLIT}	Submersed plant biomass per littoral area	g·m ⁻²	2.9	0.0 - 16.6
PLNT _{COV}	Plant cover as % of total lake area	%	35	2 - 100
BENTHOS	Benthic biomass per euphotic zone area	g·m ⁻²	2.5	0.5 - 7.9

readily identifiable by field personnel (i.e. tall emergent plants; floating varieties; deep or shallow submersed forms). Within each plant class, collection sites were determined through a random selection of points using a 0.5 cm grid overlain a 1:5000 scale outline map. Field sampling took place between late-July and mid-August, utilizing a surface deployed biomass sampler (see Section 3, this thesis). Macrophytes were subsequently identified to species, and weights obtained by oven drying at 80° C to a constant weight.

Benthic collections were made during the midsummer period with a Ponar grab which sampled an area of 231 cm². A depth stratified, random sampling design was employed. For 10 lakes, samples were taken at depths of 1, 2, 3, 5, 7, 10, 15, and 20 m, and at maximum depth, along three or more randomly located transects. For the remaining nine lakes, the reduced effort design recommended by Cullis (1986) was adopted to determine total sample number, with samples collected at randomly chosen locations at the 1 m depth, at mid-thermocline depth, and in the deep profundal region. Organisms were separated from the sediments, then pooled to determine the total wet weight for each lake.

Prior to statistical analysis, values for all variables were Log₁₀ transformed to reduce heteroscedasticity and linearize the relationships, while maintaining agreement with the original TSI models. SAS was employed for all statistical procedures (SAS Institute Inc. 1987).

1.4 Results and Discussion

1.4.1 Initial Modifications to Carlson's TSI

Carlson's (1977) TSI models provide a means of estimating the trophic status of a lake, with knowledge of one of three input parameters: Secchi transparency (SD), total phosphorus

concentration (TP), or chlorophyll *a* concentration (CHL). The TSI was originally scaled to span a trophic range of 0 to 100, corresponding to a theoretical range of lake SD of 64 m to 0.063 m, through the equation

$$2) \quad TSI_{SD} = 60 - 33.22 \text{ Log (SD)}.$$

An examination of data from a variety of sources (Armstrong and Schindler 1971; Ryan 1980; Fee et al. 1989; other unpublished data) indicated that the TSI_{SD} for lakes of northwestern Ontario commonly ranges from an index value of 20 (equivalent to a SD of 16 m) to an index value of 70 (equivalent to a SD of 0.5 m). For the exclusive modelling of these Ontario lakes, the TSI could be rescaled to span only this range of values. The drawback of using a custom scaled TSI is that direct comparisons with lakes of other regions would no longer be possible; for this reason, it was decided to retain the original scale.

TSI values were initially computed for each lake using the equations developed by Carlson (1977) for each of the three input variables. Plotted values for TSI_{SD} versus TSI_{CHL} demonstrated a 1:1 relationship, however TSI_{SD} was consistently greater than that expected for a given value of TSI_{TP} . Walker (1979) noted a similar bias for Connecticut lakes, while Osgood (1982) reported the reverse bias for lakes of the Twin Cities area of Minnesota.

For the TSI to have regional applicability, the equations must reflect the observed relationship among variables across the locale in question. If the relationships differ from those reported by Carlson (1977), adjustments would be required. Predictive equations among SD, TP, and CHL were therefore determined for lakes of the present study. For confirmation purposes, a second lake set from northwestern Ontario (Ryan 1980) was also examined. A comparison of these data with Carlson's (1977) values (Table 1.2) suggests that a recalibration of the TSI is necessary.

Table 1.2: Least squared regression parameters for SD, TP, and CHL, as reported by Carlson (1977) and determined from two northwestern Ontario lake sets. Sample size (n) and model significance (p), where known, are indicated in brackets below the parameter values.

Source	Log(SD) = $a + b\text{Log}(\text{TP})$			Log(SD) = $a + b\text{Log}(\text{CHL})$			Log(CHL) = $a + b\text{Log}(\text{TP})$		
	a	b	r^2	a	b	r^2	a	b	r^2
Carlson (1977)	1.68 (n=61)	-0.98	0.89	0.89 (n=147)	-0.68	0.93	-1.06 (n=43)	1.45	0.85
This Study	1.65 (n=19; $p < 0.001$)	-1.08	0.51	0.73 (n=19; $p < 0.0001$)	-0.68	0.65	-0.55 (n=19; $p < 0.05$)	0.87	0.23
Ryan (1980) ¹	1.57 (n=39)	-1.07	0.70	0.48 (n=41; $p < 0.0001$)	-0.71	0.42	-0.81 (n=20)	0.88	0.70

¹parameters for SD vs CHL calculated from data provided; TP represents mean summer phosphorus concentration

The slope of the regression between SD and TP for lakes of this study (Figure 1.1) is almost identical to that reported by Ryan (1980). Carlson (1977) reports a lesser slope for his continental lake set, indicating that more light is attenuated per unit of phosphorus in our northern lakes. Conversely, the relationship between SD and CHL (Figure 1.2) is a near perfect match with that reported by Carlson (1977), and it also closely resembles that calculated from Ryan's (1980) data.

On the basis of these comparisons, the relationships presented in Figure 1.1 and Figure 1.2 are considered to acceptably model these variables for lakes of northwestern Ontario, and through extension, other lakes of the Precambrian Shield. With this information, it is possible to produce a regionally adjusted TSI which would allow the modelling of trophic status through knowledge of either phosphorus or chlorophyll concentration, in addition to Secchi depth. This is accomplished by substituting the term 'log(SD)' in Eq. 2 with the predictive equation presented in Figure 1.1, to produce

$$3) \quad TSI_{TP} = 5.28 + 35.96 \text{ Log}(TP)$$

and performing a similar substitution using the equation presented in Figure 1.2, to produce

$$4) \quad TSI_{CHL} = 35.80 + 22.56 \text{ Log}(CHL).$$

When derived from either of the three parameters, TSI values should be equivalent for a lake. However, incongruities are at times noted (Carlson 1977, Osgood 1982), which are obvious as residuals from the line of 1:1 slope (Figure 1.3(A)). Such differences, when present in a regionally corrected model (as accomplished here), are attributable to incorrect model specification, measurement error, or interrelationships with unaccounted variables (Nicholls and Dillon 1978; Walker 1979). The magnitude of these incongruities were determined by subtracting individual TSI values from a simple arithmetic mean TSI, computed as

$$5) \quad TSI_{MEAN} = (TSI_{SD} + TSI_{TP} + TSI_{CHL}) / 3.$$

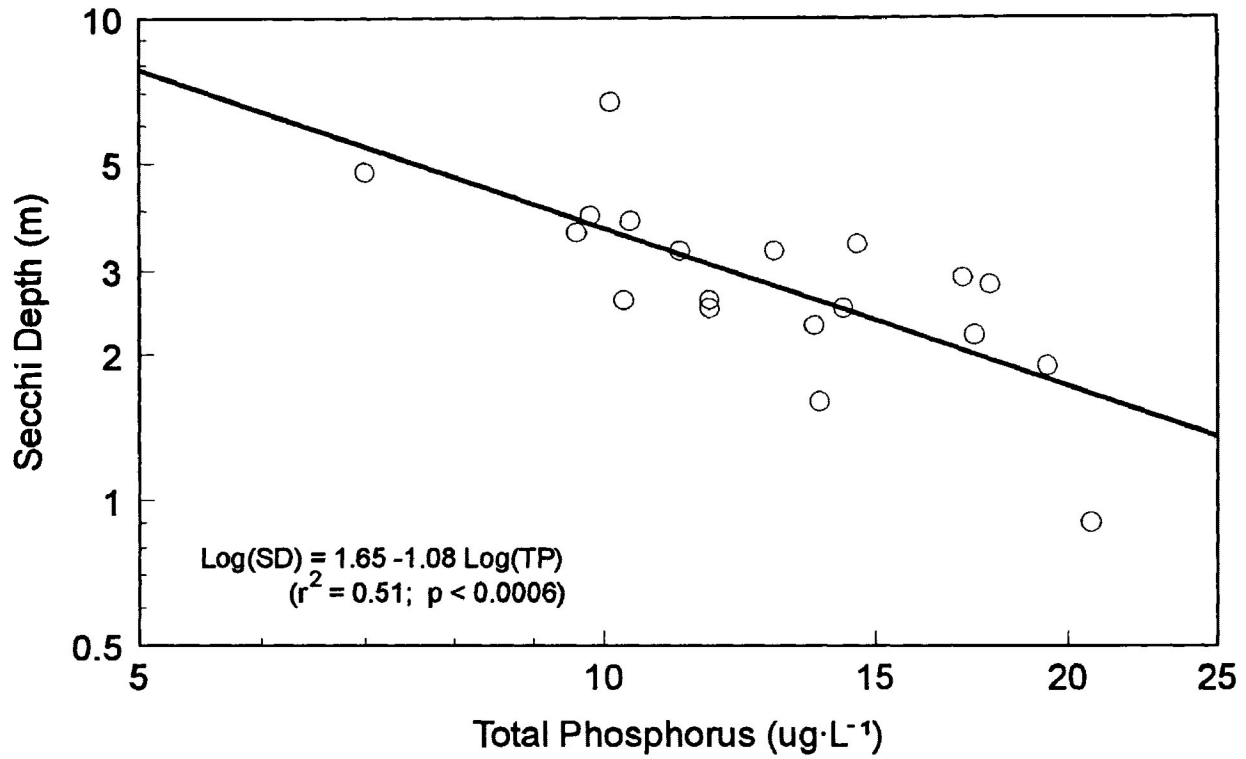


Figure 1.1 Summer Secchi disk transparency versus total phosphorus concentration at spring overturn, for lakes of northwestern Ontario.

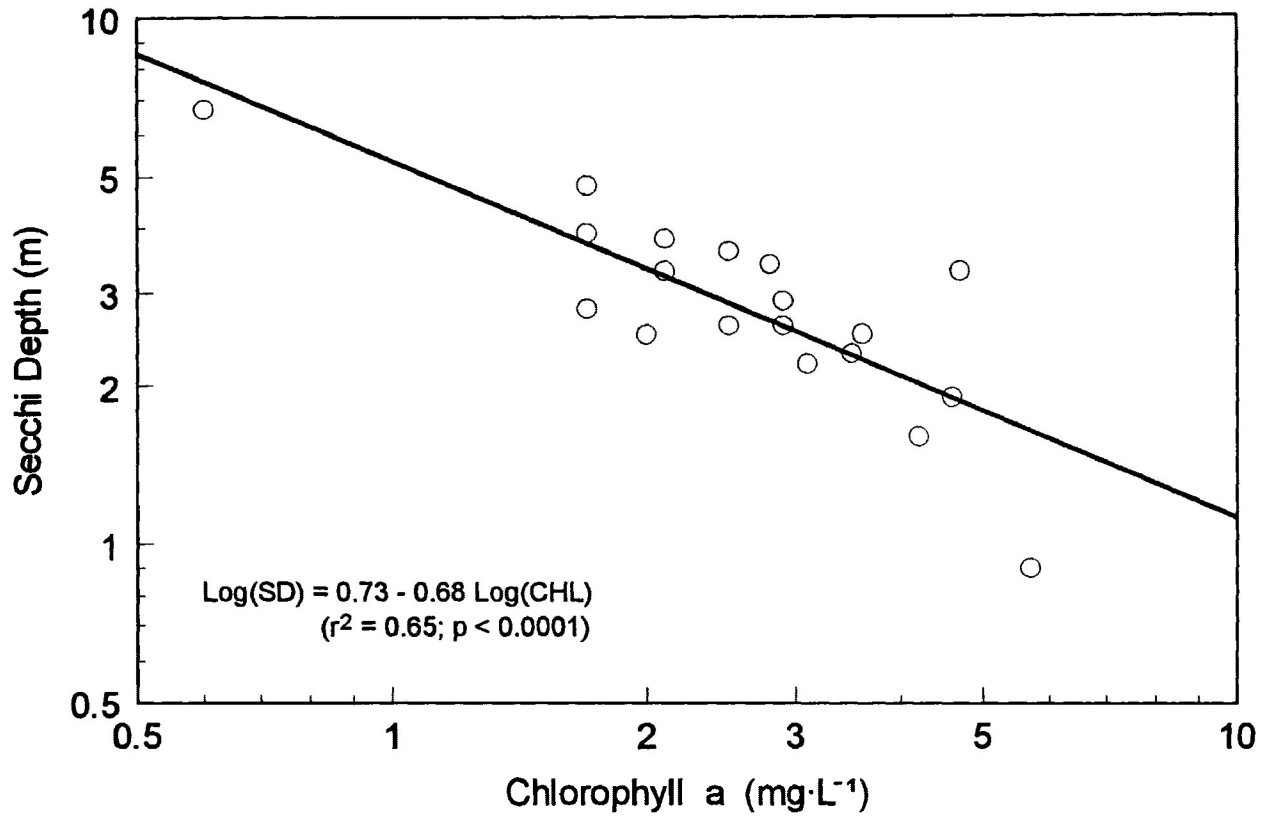


Figure 1.2 Summer Secchi disk transparency versus summer chlorophyll *a* concentration, for lakes of northwestern Ontario.

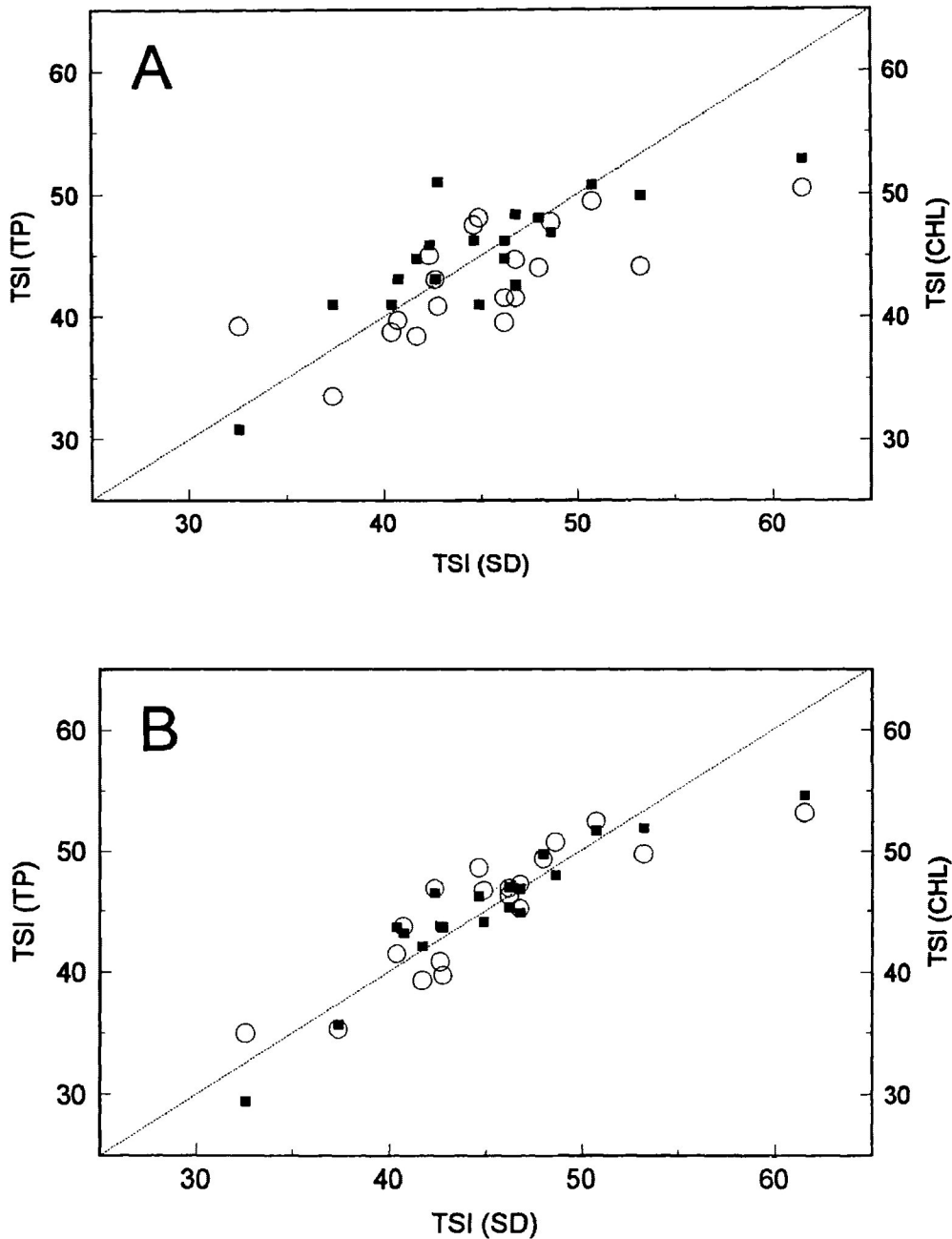


Figure 1.3 Values for TSI_{SD} versus those calculated using TSI_{TP} and TSI_{CHL} , illustrating deviation of points from the line of 1:1 slope. TSI_{TP} is plotted as open circles; TSI_{CHL} is plotted as solid squares. Values for (A) were determined from simple models (Eq. 2, 3, and 4). Values for (B) were determined from two-variable models which corrected for water colour or DOC (Eq. 2, 16, 18), and demonstrate an improvement in model fit.

TSI_{MEAN} would average the error associated with the individual parameters, and would represent the most robust estimate of trophic state. Factors contributing to differences from this value, as evident through simple correlation analysis, relate mainly to water colour and the occurrence of aquatic macrophytes (Table 1.3). Adjustments can be made to correct for these influences, which would be expected to improve model performance.

1.4.2 Corrections for Water Colour

Secchi transparency is a function of water colour and inorganic turbidity, in addition to algal density (Tyler 1968; Brezonik 1978). Low transparency often results from non-chlorophyll sources, as evident in dystrophic lakes highly stained by lignins and organic acids, or those in which suspended sediments or colloidal materials are abundant. Lakes with these attributes, such as the highly turbid glacial lakes of Alaska, experience reduced concentrations of chlorophyll per unit phosphorus (Koenings and Edmundson 1991). The same may be true of highly coloured lakes, which are often small and shallow, with extensive littoral areas (Rasmussen et al. 1989). Chow-Fraser and Duthie (1983) cautioned that true chlorophyll levels may be much lower than estimated by phosphorus in dystrophic lakes of this region.

It follows, then, that lakes with high levels of colour (indicated by a high value for DOC) demonstrate inflated TSI_{SD} values when compared with TSI_{MEAN} , while the reverse is true for low coloured lakes (Figure 1.4). Lakes exhibiting only a slight degree of dystrophy (i.e. $DOC < 8 \text{ mg}\cdot\text{L}^{-1}$) may benefit from an upwards scaling of TSI_{SD} , while lakes exhibiting a high degree of dystrophy (i.e. $DOC > 15 \text{ mg}\cdot\text{L}^{-1}$) may benefit from a downward scaling. A comparison of TSI_{SD} minus TSI_{MEAN} for these three groups indeed confirms that the highly dystrophic group has significantly higher values than the remainder (Duncan's multiple range test; $p < 0.05$).

Table 1.3: Significant correlations between abiotic and plant biomass parameters, and the difference between the various TSI values and TSI_{MEAN} . Significance levels are indicated as * $p < 0.05$; ** $p < 0.01$.

TSI Difference	Correlations (r)							
	COLOR	TURB	DOC	%LITT	AREA	PLNT _{ALL}	PLNT _{LIT}	PLNT _{SUBLIT}
$TSI_{SD} - TSI_{MEAN}$	0.59**	0.52*	0.63**	0.51*				
$TSI_{CHL} - TSI_{MEAN}$					0.51*	-0.53*	-0.56*	-0.48*
$TSI_{TP} - TSI_{MEAN}$				none significant				

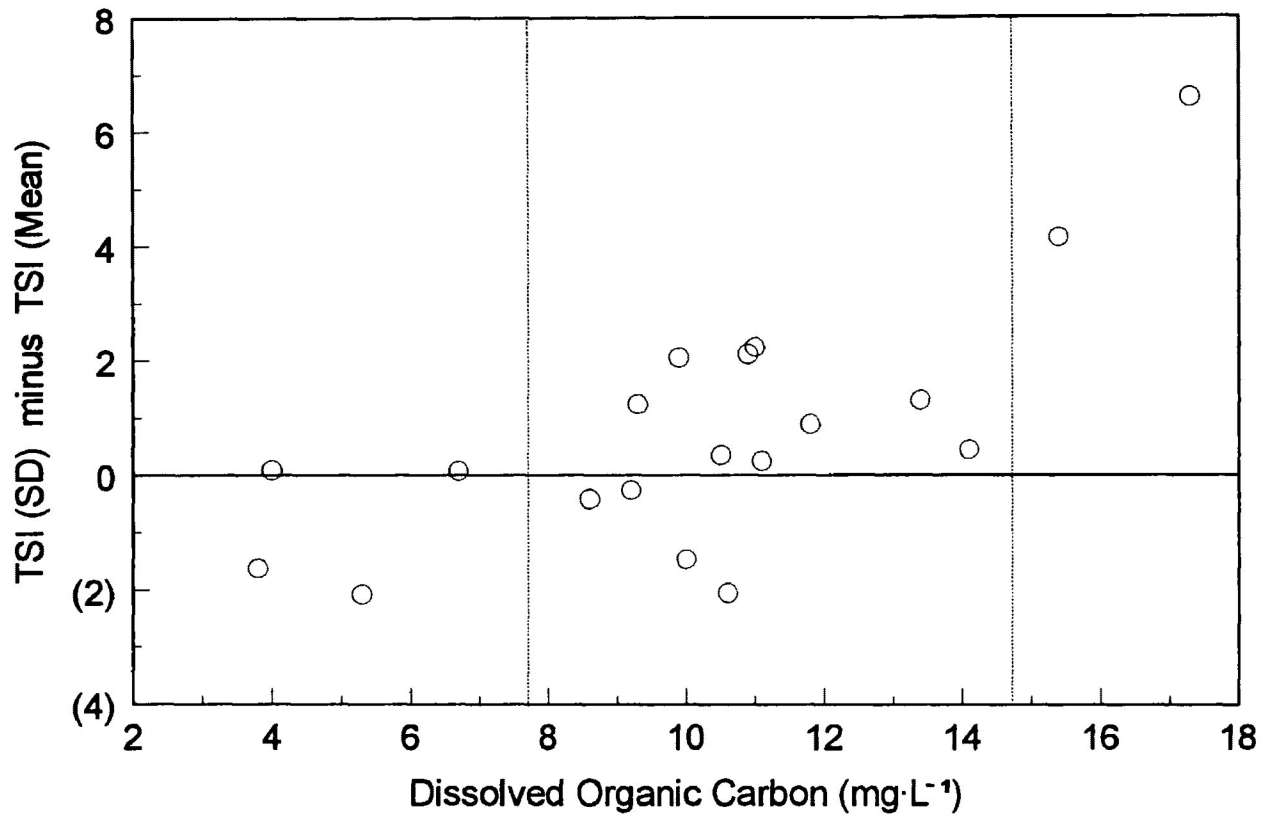


Figure 1.4 The difference between TSI_{SD} and TSI_{MEAN} , plotted against DOC. Negative values at low DOC concentrations indicate an underestimation of trophic status by TSI_{SD} , with the reverse occurring at high DOC concentrations.

Brezonik (1978) and Walker (1979) suggested that a correction factor be applied for the effects of nonalgal materials on the transparency measurement, and provided adjustment terms suitable for highly coloured Florida lakes (average 122 Pt·L⁻¹) and slightly coloured Connecticut lakes (average <25 Pt·L⁻¹), respectively. Neither of these adjustments were suited to lakes of northwestern Ontario, which fell midway between these two extremes, with an average colour of approximately 40 Pt·L⁻¹.

Brezonik (1978) suggested that an equation similar in form to (1) be used to estimate the transparency of a colourless lake, and that this value then be used in trophic classifications rather than the measured transparency. While Eq. (1) demonstrates a very good fit, it is apparent that the maximum possible transparency in a colourless lake would be 7.4 m; values far in excess of this have been measured in oligotrophic lakes of the Precambrian Shield.

An alternative approach would be to compensate for this effect by adding a term for water colour to our original regression models (Table 1.4). These revised models (Eq. 6,7) reveal that an additional 24% and 22% of the variation between SD and TP, and 14% and 19% of the variation between SD and CHL, is explained by COLOR and DOC, respectively. Canfield and Hodgson (1983) presented an equation of striking similarity to (9), calculated for 205 Florida lakes, as

$$\text{Log}(\text{SD}) = 0.87 - 0.37 \text{ Log}(\text{CHL}) - 0.28 \text{ Log}(\text{COLOR}) \quad (R^2 = 0.78).$$

They selected this as the best empirical model for SD, and considered it to represent the limit of the predictive abilities of this type of model. Replacing COLOR with DOC results in an equation with even more predictive power, and may in fact be preferable for trophic modelling.

These multiple regression equations can be substituted for the 'log(SD)' term in Eq. (2) to produce a set of refined TSI_{TP} and TSI_{CHL} models (Table 1.5 - Eq. 15, 16, 17, 18). The addition of the DOC

Table 1.4: A comparison of simple and select multiple regression models for the primary trophic parameters, including model R^2 , overall model significance (Prob>F), and the coefficient of variation (CV) for each. The significance values (p) of the individual regression parameters are indicated beneath the equations, in brackets.

Regression Model	R^2	Prob>F	CV
5) $\text{Log}(\text{SD}) = 1.65 - 1.08 \text{Log}(\text{TP})$ ($p < 0.001$)	0.51	0.0006	30.0
6) $\text{Log}(\text{SD}) = 1.48 - 0.30 \text{Log}(\text{TP}) - 0.72 \text{Log}(\text{DOC})$ ($p < 0.325$) ($p < 0.003$)	0.73	0.0001	23.1
7) $\text{Log}(\text{SD}) = 1.35 - 0.37 \text{Log}(\text{TP}) - 0.33 \text{Log}(\text{COLOR})$ ($p < 0.187$) ($p < 0.002$)	0.75	0.0001	22.2
8) $\text{Log}(\text{SD}) = 0.73 - 0.68 \text{Log}(\text{CHL})$ ($p < 0.001$)	0.65	0.0001	25.4
9) $\text{Log}(\text{SD}) = 1.00 - 0.34 \text{Log}(\text{CHL}) - 0.27 \text{Log}(\text{COLOR})$ ($p < 0.028$) ($p < 0.005$)	0.79	0.0001	20.1
10) $\text{Log}(\text{SD}) = 1.17 - 0.39 \text{Log}(\text{CHL}) - 0.57 \text{Log}(\text{DOC})$ ($p < 0.003$) ($p < 0.001$)	0.84	0.0001	17.8
11) $\text{Log}(\text{SD}) = 1.09 - 0.40 \text{Log}(\text{CHL}) - 0.26 \text{Log}(\text{COLOR}) - 0.07 \text{Log}(\text{PLNT}_{\text{COV}})$ ($p < 0.007$) ($p < 0.003$) ($p < 0.035$)	0.85	0.0001	17.8
12) $\text{Log}(\text{SD}) = 1.01 - 0.34 \text{Log}(\text{CHL}) - 0.29 \text{Log}(\text{COLOR}) - 0.06 \text{Log}(\text{PLNT}_{\text{SUBLT}})$ ($p < 0.011$) ($p < 0.001$) ($p < 0.013$)	0.87	0.0001	16.7
13) $\text{Log}(\text{CHL}) = -0.55 + 0.87 \text{Log}(\text{TP})$ ($p < 0.037$)	0.23	0.0367	47.8
14) $\text{Log}(\text{CHL}) = -0.79 + 1.16 \text{Log}(\text{TP}) - 0.17 \text{Log}(\text{PLNT}_{\text{LT}})$ ($p < 0.008$) ($p < 0.055$)	0.39	0.0181	43.8

or COLOR correction term results in an obvious improvement in the correspondence of the different TSI models (Figure 1.3(B)). The magnitude of the residual values from the line of 1:1 slope is substantially less than that noted from the simpler, non-colour corrected model (paired *t*-tests; $p < 0.0002$).

1.4.3 Corrections for Aquatic Macrophyte Abundance

The negative relationship between macrophyte abundance and phytoplankton biomass is well documented (Hassler and Jones 1949; Gasaway and Drda 1978; Mitchell 1989; Jones 1990). Suspected causes include the secretion of allelopathic substances by macrophytes, which suppress the growth of phytoplankton (Phillips et al. 1978; Crawford 1979; Wium-Andersen et al. 1982). Macrophytes may also act as daytime refuges to large-bodied zooplankton, reducing their vulnerability to fish predation (Savino and Stein 1982, 1989; Timms and Moss 1984). As the abundance of large zooplankton increases, more algae is consumed, and epilimnetic chlorophyll concentrations may be lowered (Pace 1984; Kitchell et al. 1988; Evans 1990). Additionally, stands of macrophytes with dense canopies may reduce subsurface light levels sufficiently in some waters to retard the production of phytoplankton (Westlake 1964; Titus and Adams 1979).

The antagonism between macrophytes and phytoplankton may also be related to competition for a finite and limited supply of nutrients. While rooted aquatic plants obtain phosphorus primarily from the sediments, they may also take a portion from the water column (Best and Mantai 1978; Carignan and Kalff 1980; Balls et al. 1985; Chambers et al. 1989). Non-rooted plant varieties (e.g. *Ceratophyllum demersum*) are capable of extracting large quantities of nutrients from the water (Phillips et al. 1978). The epiphytes associated with aquatic macrophytes may be of even greater importance. Epiphytic production may meet or exceed the production of phytoplankton

Table 1.5: TSI equations, based on a Secchi transparency scale, and optimized for lakes of northwestern Ontario. Within each group, equations are listed in order of improved model fit, as measured by R^2 (as cited in Table 1.4). Correlation coefficients (r) reveal the relationship between the various models and benthic biomass measured across the euphotic zone (BENTHOS). Significance levels are indicated as * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

TSI Equations	BENTHOS Correlations
2) $TSI_{SD} = 60 - 33.22 \text{ Log}(\text{SD})$	0.53*
3) $TSI_{TP} = 5.28 + 35.96 \text{ Log}(\text{TP})$	0.59**
15) $TSI_{TP} = 10.75 + 10.01 \text{ Log}(\text{TP}) + 23.89 \text{ Log}(\text{DOC})$	0.61**
16) $TSI_{TP} = 15.00 + 12.15 \text{ Log}(\text{TP}) + 11.07 \text{ Log}(\text{COLOR})$	0.62**
4) $TSI_{CHL} = 35.80 + 22.56 \text{ Log}(\text{CHL})$	0.55*
17) $TSI_{CHL} = 26.88 + 11.24 \text{ Log}(\text{CHL}) + 9.03 \text{ Log}(\text{COLOR})$	0.61**
18) $TSI_{CHL} = 21.20 + 12.87 \text{ Log}(\text{CHL}) + 19.09 \text{ Log}(\text{DOC})$	0.63**
19) $TSI_{CHL} = 23.92 + 13.15 \text{ Log}(\text{CHL}) + 8.59 \text{ Log}(\text{COLOR}) + 2.36 \text{ Log}(\text{PLNT}_{\text{COV}})$	0.63**
20) $TSI_{CHL} = 26.33 + 11.27 \text{ Log}(\text{CHL}) + 9.52 \text{ Log}(\text{COLOR}) + 1.90 \text{ Log}(\text{PLNT}_{\text{SUBLIT}})$	0.70***

in a lake (Wetzel 1964), and can contribute to 70-85% of the total lake primary production (Wetzel 1990). Epiphytes can better utilize available phosphorus to increase their biomass than can phytoplankton (Sand-Jensen and Sondergaard 1981). An abundance of macrophytes could imply an abundance of epiphytes, and hence the possibility of major competition with phytoplankton for available nutrients.

It follows that a corrective term for macrophytes may improve the relationship between CHL and TP, as suggested by Canfield (1983). For global or continental lake sets, the slope of the simple regression equation between CHL and TP varies from 1.45-1.47 (Dillon and Rigler 1974; Jones and Bachman 1976; Carlson 1977). More recently, it has been demonstrated that a sigmoid relationship exists over a global range of values (McCauley et al. 1989). On a narrower scale, though, from TP ~ 6 to $60 \mu\text{g}\cdot\text{L}^{-1}$ (which spans this lake set) algal biomass appears to increase at a relatively constant rate (Watson et al. 1992). Prairie et al. (1989) recently assembled a wide-ranging data set which revealed a much flatter slope than the previous studies, of about 0.87. This value is nearly identical to that reported from both the present study and Ryan (1980) (Table 1.2). Similar low slopes have been reported for other lakes of North America (e.g. Hern et al. 1981; Canfield 1983), but these are at least partially explained by a low nitrogen to phosphorus (TN:TP) ratio (i.e. < 10). Lakes of the Precambrian Shield commonly have a TN:TP ratio exceeding 15 (Dillon and Rigler 1974; Ryan 1980), which past studies have shown to be limited by TP alone (Sakamoto 1966; Chiandani and Vighi 1974). Prairie et al. (1989) demonstrated that the regression coefficients appear to shift with changing ratios of TN:TP, and for a ratio of 15 or higher they predict a slope much greater than 0.87. It appears, then, that the phytoplankton produced per unit phosphorus in our northern lakes is substantially less than expected on the basis of the Prairie et al. (1989) model or that predicted from many global lake sets.

Multiple regression analysis confirms that macrophytes have a significant effect on the relationship between CHL and TP. An additional 16% of the variance in CHL is explained when the total plant biomass per unit littoral area ($PLNT_{LITT}$) is included as a dependant variable, in combination with TP (Table 1.4 - Eq.14). The inclusion of other measures of plant abundance also resulted in improvements to R^2 , but to a lesser degree than $PLNT_{LITT}$.

It is not unexpected, then, that the differences observed between TSI_{CHL} and TSI_{MEAN} are also associated with the presence and abundance of aquatic macrophytes (Figure 1.5). Lake area represents an additional factor to consider (Table 1.3), but this is thought to be related to the fact that large lakes tend to have fewer submersed plants per unit area than do small ones (Duarte et al. 1986). TSI_{CHL} appears to overestimate the trophic status of lakes relatively depauperate of plants (i.e. $< 4 \text{ g}\cdot\text{m}^{-2}$ dry weight), as evident by the positive values for TSI_{CHL} minus TSI_{MEAN} . The mean for these values is significantly higher (Duncan's multiple range test, $p < 0.05$) than for lakes which support a greater abundance of macrophytes.

An adjustment in TSI_{CHL} to account for macrophyte abundance is then justified. However, a redefinition of the relationship between SD and CHL through the addition of a macrophyte term alone does not significantly improve the SD prediction (data not shown). When the variable COLOR is also included, though, $PLNT_{COV}$ and $PLNT_{SUBLIT}$ both result in an enhanced model (Table 1.4 - Eq. 11, 12). These models may then be substituted into Eq. (2) to produce TSI_{CHL} models of even greater precision (Table 1.5 - Eq.19, 20).

Obtaining biomass estimates for aquatic plants is a time-consuming and costly exercise, even though low effort approaches have been defined (Schloesser and Manny 1984; Duarte 1987;

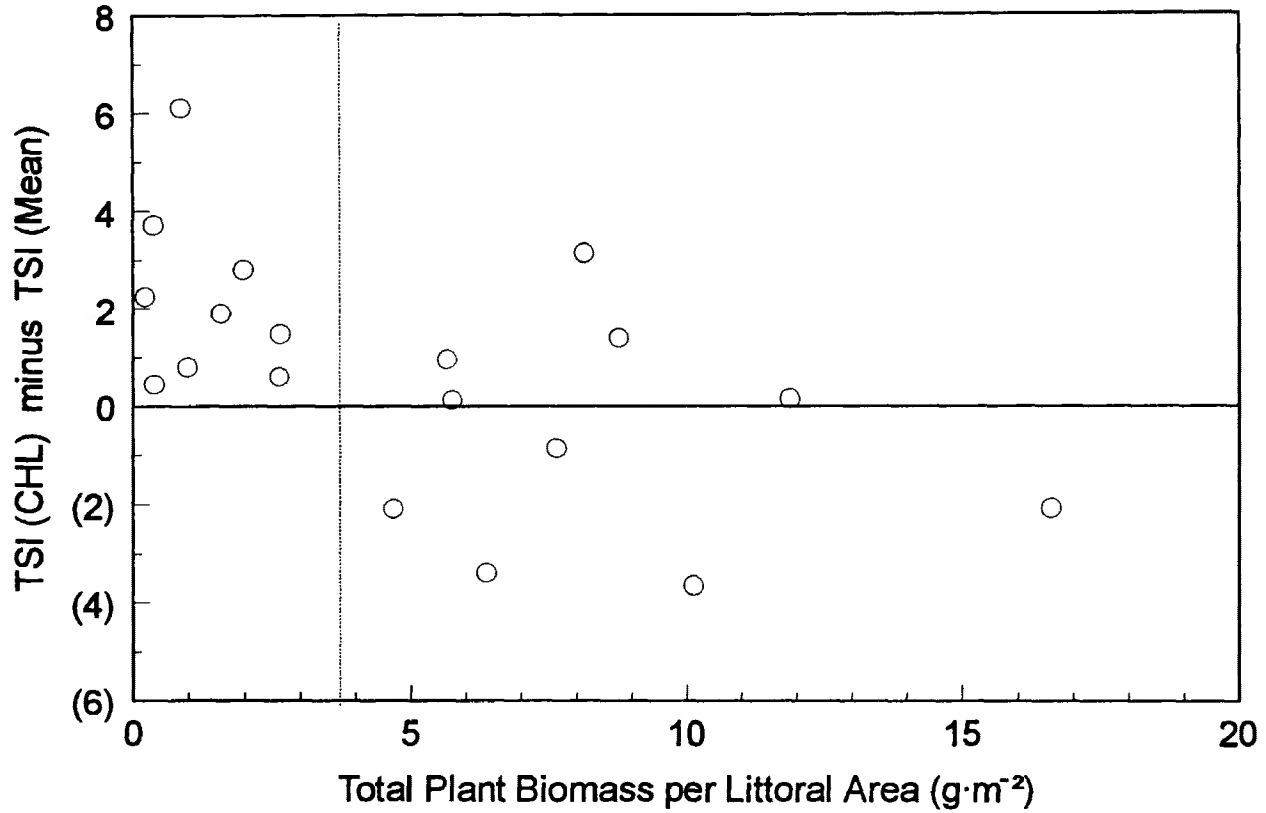


Figure 1.5 The difference between TSI_{CHL} and TSI_{MEAN} , plotted against $PLNT_{LIT}$. Positive values at low levels of macrophyte abundance indicate an overestimation of trophic status by TSI_{CHL} , with the reverse occurring at high levels of macrophyte abundance.

Canfield et al. 1990; see also Section 2 & 3, this thesis). In addition, it is apparent that the complex models which consider macrophyte abundance (Eq. 11, 12) show minimal R^2 improvement over the simpler CHL-DOC model (Eq. 10). The high significance of DOC, when combined with CHL, may relate to the fact that growing and decaying macrophytes secrete DOC, and their presence in a lake raises the concentration of this substance in the water column (Wetzel and Manny 1972). The CHL-DOC model may therefore integrate the effects of both macrophyte production and water colour, and through this process explains nearly the same variance in SD as do the more complex models. DOC is a readily obtainable and inexpensive measurement, and demonstrates high temporal stability. On this basis, the CHL-DOC model appears to be a suitable compromise when estimates of plant biomass are unobtainable.

1.4.4 A Test of Model Performance

A true measure of secondary or tertiary production would be the preferred measure of performance for the TSI models. If lacking, the standing stock of macrobenthos may be a viable alternative measure. Benthic biomass is driven by lake trophic variables (Dermott et al. 1977; Hanson and Peters 1984; Rasmussen and Kalff 1987), and is highly correlated with annual secondary production (Plante and Downing 1989) and tertiary (fish) production (Matuszek 1978). On this basis, benthic biomass from the euphotic zone (BENTHOS) was used as a response variable by which to judge the relative utility of the various TSI models.

In general, the performance of the TSI models, as measured by changes in the correlation coefficients for BENTHOS, improves with an increase in model R^2 (Table 1.5). It is apparent that the more highly developed the TSI model, the better it predicts benthic biomass. The improvement is most profound for TSI_{CHL} . When expressed as a regression model, the addition of the COLOR

and $PLANT_{\text{SUBLIT}}$ term (Eq. 20) explains 19% more of the variance in BENTHOS than does the simple CHL model (Eq. 4).

These results suggest that better models of lake trophic status have indeed been developed. However, in addition to contributing to total primary productivity, aquatic plants function as a habitat variable, and this effect may also account for some of the apparent model improvement. Macrophytes provide both food and refugia for benthos, and the presence of plants is known to affect the distribution and increase the standing stocks of macroinvertebrates (Watkins et al. 1983; Schramm and Jirka 1989; Chilton 1990; Hanson 1990).

Canfield et al. (1983) provided an alternative means for adjusting lake trophic status to account for aquatic macrophytes. They suggested correcting the total phosphorus value to include the phosphorus bound up in the plants. The adjustment is made by determining the biomass of different plant species and their percent phosphorus content, then calculating the total phosphorus contained in the plants and adding this to that measured in the water to obtain a value termed 'water column phosphorus' (WCP).

A review of the data presented by Canfield et al. (1983) indicates that, on average, the percent phosphorus content of submersed macrophytes is 0.223% of dry weight. Applying this value, it is possible to estimate the phosphorus contained by plants in the present lake set, and adjust the total phosphorus value in a manner similar to that explained above.

Benthic biomass can once more be used as an output measure to assess the WCP model. Correlations of WCP with BENTHOS ($r=0.45$) reveal a lesser degree of fit than observed with the simplest TSI_{TP} model (Eq. 3), which indicates that WCP performs relatively poorly as a trophic

status indicator for lakes of the Precambrian Shield. Canfield et al. (1983) acknowledged, however, that this approach would be most useful for assessing shallow, macrophyte dominated lakes, and would have little effect when macrophyte concentration was less than 1 g dry weight·m⁻³. As approximately one half of the lakes of this study fit this description, they obviously do not represent an appropriate test set for the WCP model.

1.5 Conclusions

1) Relationships between trophic parameters for lakes of northwestern Ontario differ from those previously noted for global or continental lake sets. In comparison, the Ontario lakes demonstrate: a) more light attenuation per unit phosphorus, and b) less chlorophyll production per unit phosphorus.

2) Water colour is highly correlated with all three trophic parameters, and influences the Secchi transparency - phosphorus and Secchi transparency - chlorophyll relationships. The inclusion of a term for water colour or dissolved organic carbon in multiple regression models explains 14-24% more of the variance in these relationships.

3) The abundance of aquatic macrophytes affects the relationships between the trophic parameters. The total plant biomass within the littoral area, when combined with phosphorus, explains an additional 16% of the variance in chlorophyll. The Secchi transparency - chlorophyll model, already improved through consideration of water colour, demonstrates further improvement through the addition of a plant biomass term. Dissolved organic carbon appears to integrate the effect of both water colour and plant abundance, and may be substituted for these variables in an alternative model when plant biomass estimates are unavailable.

4) TSI equations, styled after those of Carlson (1977), have been recalibrated for application to lakes of northwestern Ontario and, through extension, the entire Laurentian Precambrian Shield. The addition of corrective terms to adjust for the effects of water colour and aquatic macrophyte abundance result in more agreement between models. The mean TSI value, an average of that calculated using different trophic input parameters, provides a robust description of lake trophic status.

5) The standing stock of benthos represents an appropriate response variable by which to measure lake trophic status. When judged against this standard, the improved performance of the TSI models which consider water colour and aquatic macrophyte abundance is confirmed.

2. Mapping aquatic macrophytes through digital image analysis of aerial photographs: an assessment

2.1 Abstract

Distributional maps of aquatic vegetation are commonly produced from aerial photographs using visual interpretive techniques. Image analysis represents an alternative technique through which this process can be automated, using readily available computer hardware and software. The photographs are first digitized, and the system trained to recognize a set of spectral patterns or 'signatures' which are unique for particular macrophyte species or groups. All pixels which comprise the image are then classified on the basis of their conformance with these signature values; this results in a map or GIS overlay of aquatic plant distribution. The boundaries of plant beds can be defined with precision using this method, which contributes to a more accurate estimation of total plant cover and production. Submersed species proved most difficult to classify, especially in shallow lakes where highly reflective substrates confounded the signature selection process. In contrast, classification to the species level is feasible for some floating-leafed and emergent forms, and the further partitioning into density classes may also be possible. However, at this level of detail, spectral signatures may not be transportable over space or time. A detriment to the approach is the steep learning curve associated with image analysis software. Nevertheless, once versed in its operation, vegetation maps can often be produced with more accuracy and efficiency than with the visual interpretive method.

2.2 Introduction

Aerial photography has become increasingly popular as a tool by which to map aquatic vegetation, as it can be obtained rapidly and at relatively low cost, and provides a permanent record of current conditions (e.g. Andrews et al. 1984; Schloesser et al. 1988). Visual qualities such as shape, tone, and texture are used to distinguish vegetation from other features in the photographs, and to identify particular taxa and define the boundaries of individual plant beds. This information is manually recorded by the photo-interpreter on an outline map of the water body to produce a distributional map of the macrophytes. However, even with a knowledge of photo interpretation techniques and a familiarity with local field conditions, there is much room for error in this process. It has been reported that genera of submersed macrophytes are correctly recorded only 56%-70% of the time using this approach (Macomber and Fenwick 1979; Haegele and Hamey 1980; Schloesser et al. 1987). In addition, the manual preparation of maps is exceedingly time-consuming, and while scale-dependant, the boundary resolution of plant beds is fairly limited.

Forsgren and Wallsten (1987) introduced a means of automating this process, which promised higher precision and shorter evaluation times than the manual approach. Their technique employed sophisticated scanning equipment and a mini-computer, along with some simple image processing algorithms, to aid in the classification and mapping functions. The advantages include improved map resolution through the pixel-level delineation of boundaries of plant beds, and increased accuracy through the identification of macrophyte taxa based on differences in tone and shading that are near-indistinguishable to the human eye.

Recent advances in technology allow the application of Forsgren and Wallsten's (1987) technique using affordable, off-the-shelf computer hardware and software (Welch 1989). The process can be considerably refined and automated, which makes it an increasingly attractive alternative to the

manual mapping technique, feasible even for small-scale studies. Three steps are involved in this operation, beginning with an analog-to-digital conversion of the colour aerial photographs. This is accomplished through use of an optical-mechanical scanner or video digitizer, which produces a digital image of the scene which is recognizable to the computer.

Secondly, image processing software is employed to enhance the image and extract the required thematic information, which in this case are regions of vegetative cover, classified to plant type. This is accomplished through analysis of the spectral characteristics of the three colour bands which comprise the image. Aquatic plants demonstrate unique spectral reflectance properties, or 'signatures', which differ subtly among taxa, and in turn differ grossly from the open water, non-vegetated areas. Once these signatures are defined for a plant species or group, all pixels across the image with similar values are assigned the same classification. The process of signature definition and pixel classification is then repeated until all macrophyte beds have been charted.

Thirdly, a digital map of the lake is generated, with the regions of aquatic plant coverage defined. This represents an overlay suitable for placement in a Geographic Information System (GIS), and when in this format distributional maps of aquatic vegetation can be selectively printed and statistics associated with the theme readily extracted.

This paper evaluates the performance of the computer image analysis approach to the classification and mapping of aquatic macrophytes. For trial purposes, colour aerial photographs were taken of two northwestern Ontario lakes that differed substantially in their depth, water colour, and plant community composition. Image analysis was utilized to classify the aquatic plants and to generate a map of their distribution. For each lake, the ability to differentiate among different types of aquatic vegetation and to accurately record their distributional patterns using this

technique is assessed. The area of plant cover and production estimates determined in this manner are compared with those obtained using the conventional, visual interpretive method. The advantages and disadvantages of the automated approach are discussed, including mapping accuracy and precision, time efficiencies, and knowledge and skills required of the operator. Other considerations which may limit its utility are noted.

2.3 Methods

Two lakes typical of the boreal forest region of Canada were selected near Thunder Bay, in northwestern Ontario. These lakes present a range of conditions through which to test the utility of the image analysis technique (Table 2.1). Walkinshaw Lake is moderately deep, with highly stained water, and dominated by floating-leafed vegetation occurring largely in shallow nearshore areas. Big Pearl Lake is shallow throughout, with quite transparent water, and with a mixture of macrophytes, including dense colonies of submersed plants occurring in the mid-basin of the lake.

Aerial photography was carried out from late July to early August, a period which corresponds with peak biomass of most macrophyte species in these lakes. Photographs were taken near high noon on clear, cloudless, and relatively wind-free days to ensure maximum light penetration. Colour infrared film was found to provide slightly better differentiation of floating and emergent plants, but true colour film was selected as the preferred film type for this study due to its superior depth penetration which rendered far better detail of submersed species. The lakes were photographed at an altitude of 280 m with a 645 format camera fitted with a 45 mm lens. This provided a scale of 1:5000, which, following a 4X enlargement of the negatives, yielded sufficient spatial resolution for identification of plant taxa (Olson 1964; Bogucki and Gruendling 1978). As an example, high tension hydro-electric lines could be readily discerned on these prints. Ground coverage of each photograph was 1120 m by 830 m.

Table 2.1: Limnological and morphometric characteristics of Walkinshaw and Big Pearl Lake.

	Walkinshaw Lake	Big Pearl Lake
Area (ha)	35.4	50.6
Mean depth (m)	3.3	1.2
Maximum depth (m)	11.7	2.8
Water colour (Pt·L ⁻¹)	71	13
Turbidity (JTU)	1.5	2.1
Secchi depth (m)	2.3	3.6 ¹

¹ Could not be measured due to shallow depth;
calculated as: $\text{Secchi depth} = 7.37 - 2.22 * \text{Log}_{10}(\text{Colour}) - 4.15 * \text{Log}_{10}(\text{Turbidity})$

Initial plant distributional maps were created through visual interpretation of these photographs. Macrophyte beds observable on the photographs were traced on a digitizing tablet, along with the lake boundary, to produce a map of plant cover. The composition and abundance of plants comprising the macrophytes were then determined through a field sampling exercise. Collections were made using a plant biomass sampler (see Section 3, this thesis), with sites located randomly along a grid within representative macrophyte beds. The plants collected were subsequently identified to species and biomass estimates obtained by oven-drying to constant weight at 80° C.

Image analysis was performed using the VGA ERDAS™ software package, which incorporates functions of both image processing and a raster-based GIS. The hardware platform comprised a 25 MHz 80386 or 50 MHz 80486 personal computer with a graphics adapter capable of displaying 1024 pixels by 768 pixels in 256 colours. Photographs were first mosaicked, then digitized using a Howtek™ or a Hewlett-Packard Scanjet IIC™ flatbed scanner. The mosaicked photograph was cropped to minimize the area surrounding the lake, and reduce the size of the digital image. A scan density of 75 pixels·cm⁻¹ was selected for the whole-lake images, and a density of 200 pixels·cm⁻¹ for the detailed mapping of the northwest bay of Walkinshaw Lake. This translates into an actual ground area covered per pixel of 0.67 m² and 0.25 m², respectively, at 1:5000 scale.

Prior to analysis, the scanned images were enhanced by examining their spectral histogram and adjusting an equalization filter to provide maximum visual colour contrast. Shorelines were then traced on-screen to produce two broad classes separating aquatic and non-aquatic regions. A mask of the non-aquatic class was generated so that terrestrial features would not complicate the classification of the aquatic vegetation.

Image data was subjected to both supervised and unsupervised multispectral classification methods. Supervised classification is an interactive process, requiring the skills of an operator knowledgeable of conditions in the field. The operator identifies training sites which represent a homogeneous example of a particular vegetation type, and the spectral characteristics of these areas are used to 'train' a classification algorithm to recognize similar vegetation at other locations within the lake. After training samples have been analyzed for each of the vegetation classes, each pixel within the image is evaluated and assigned to the class of which it has the highest likelihood of being a member.

The unsupervised classification method applied a sequential clustering algorithm, an automated procedure whereby pixels are examined sequentially, and the spectral distance calculated between the current pixel and that for previously defined clusters of pixels. Based on this spectral distance, the pixel is either placed into an existing cluster or begins a new cluster. The process continues until all pixels are examined, with clusters merged if too many are formed. To insure maximum differentiation of aquatic plants, a total of 65 clusters were initially specified. The clusters were then examined by overlaying each on an image of the original aerial photograph. Based again on the operators prior knowledge of the true plant distribution patterns, each cluster was recoded to a class indicative of a specific macrophyte taxa. Unassigned clusters were recoded as open water.

As a final step in the classification process, names were assigned to the emergent classes, and a GIS file created. Annotation was gridded to this file, and distributional maps of the aquatic macrophytes were generated by computer and output to a colour printer. Using these maps to define the boundaries of plant beds, macrophytes were again sampled for biomass estimation, using a similar sampling strategy as for the visually interpreted maps.

2.4 Results

The aquatic plant community of Walkinshaw lake was dominated by floating-leafed forms - two species of water lily, *Nymphaea odorata* and *Nuphar variegatum*, and a pondweed, *Potamogeton natans*. Occasional submersed species occur, such as *Scirpus subterminalis* and *Utricularia vulgaris*, but these were widely scattered and comprised but a small proportion of the total macrophyte biomass. Equally minor were emergent species, which consisted largely of small plots of *Eleocharis palustris* and *Typha latifolia*.

The extensive colonies of floating-leafed plants contrasted well with the darkly stained lake water on the aerial photographs. As such, they could be readily distinguished and plotted, as a group, using visual interpretive methods. The three species forming this group were often interspersed, however, and even at high magnification it was difficult to separate the taxa and define their boundaries with any level of precision. The two species of water lily were particularly difficult to differentiate, and had to be combined as a single class when a vegetation map was produced manually.

The area of plant coverage determined using the visual interpretive approach was compared with that obtained through image analysis (Table 2.2). A marked difference was noted, with a greater total coverage recorded for the floating-leafed plants when manual methods were employed. This is not unexpected, as it is impossible to resolve fine detail when visually plotting plant distribution. The boundary of plant beds are simply drawn to encompass all vegetation, and as such include open spaces where the plants are widely scattered; this ultimately inflates the overall estimate of plant area. In contrast, the computer generated map provided superb boundary detail, even of finely dissected plant beds (Figure 2.1). This detail is, of course, dependant on the resolution of the scanned image; in this instance differentiation would be to 0.67 m². The interstices between

Table 2.2: A comparison of cover estimates for different macrophytes in Walkinshaw Lake, determined through image analysis and the visual interpretive technique.

	% of Total Lake Area		Difference (%)
	Image Analysis Technique	Visual Interpretive Technique	
<i>Nymphaea odorata</i> & <i>Nuphar variegatum</i>	4.93	5.36	+ 8.7
<i>Potamogeton natans</i>	1.34	1.91	+ 42.5
Emergent spp.	0.90	0.73	- 18.9

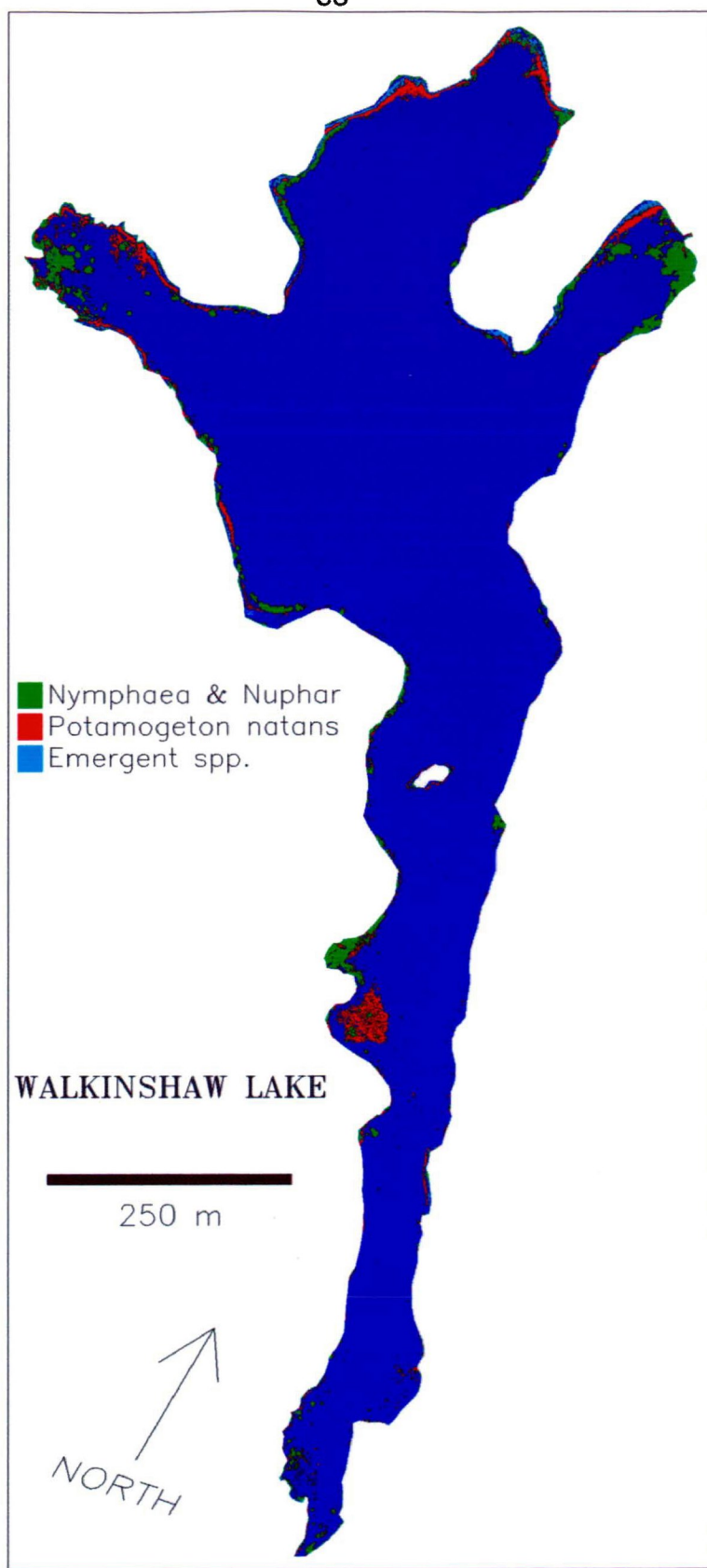


Figure 2.1 Classification map depicting the distribution of major macrophyte groups of Walkinshaw Lake.

plants are properly classed as water, hence a more accurate estimate of plant cover would be expected. In support of this, subsequent field surveys have indicated a high degree of correspondence between the actual patterns of plant distribution and that indicated on the classification map. The only exception was a tendency for the boundaries of *P. natans* beds to be slightly exaggerated in areas where lightly coloured sediments occurred.

The difference in resolution between the two mapping techniques resulted in a great disparity in plant biomass estimates (Table 2.3). Values were much lower when the boundaries of plant beds were interpreted visually. This was largely a consequence of including null samples in the biomass estimate, as would be obtained when one of the preselected (but randomly chosen) sampling points corresponded with an open space between plants. The highly detailed boundary of plant beds produced through image analysis excluded such spaces, and precluded the occurrence of null samples. The inflated areas of plant coverage recorded by the manual technique compensated somewhat for this phenomenon, but even so, the estimate of total lake production of floating-leaved plants was substantially less than that determined using the image analysis approach.

Signature values for the two species of water lily, along with *P. natans*, were sufficiently unique to allow their differentiation through image analysis. A high density scan (1 pixel = 0.25 m²) of the northwest bay of Walkinshaw Lake provides an example of classification to the species level (Figure 2.2). To determine the value of this map, a classification accuracy assessment is required (Jensen 1986; Aronoff 1989). Ideally, this would take the form of a contingency table, which compares plant classes randomly located on the ground with those represented by corresponding pixels on the classification map. While logistic considerations precluded such a formal assessment, a field cruise of the lake provided a means of subjective error assessment, and

Table 2.3: Estimates of average biomass (dry weight) within the defined plant beds and whole lake annual production for floating-leaved macrophytes in Walkinshaw Lake, as determined using distribution maps generated through image analysis versus the visual interpretive technique.

	Image Analysis Technique		Visual Interpretive Technique	
	Biomass (g·m ⁻²)	Production (kg)	Biomass (g·m ⁻²)	Production (kg)
<i>Nymphaea odorata</i> & <i>Nuphar variegatum</i>	134.2	2341.6	46.5	882.7
<i>Potamogeton natans</i>	27.2	129.2	11.2	75.6

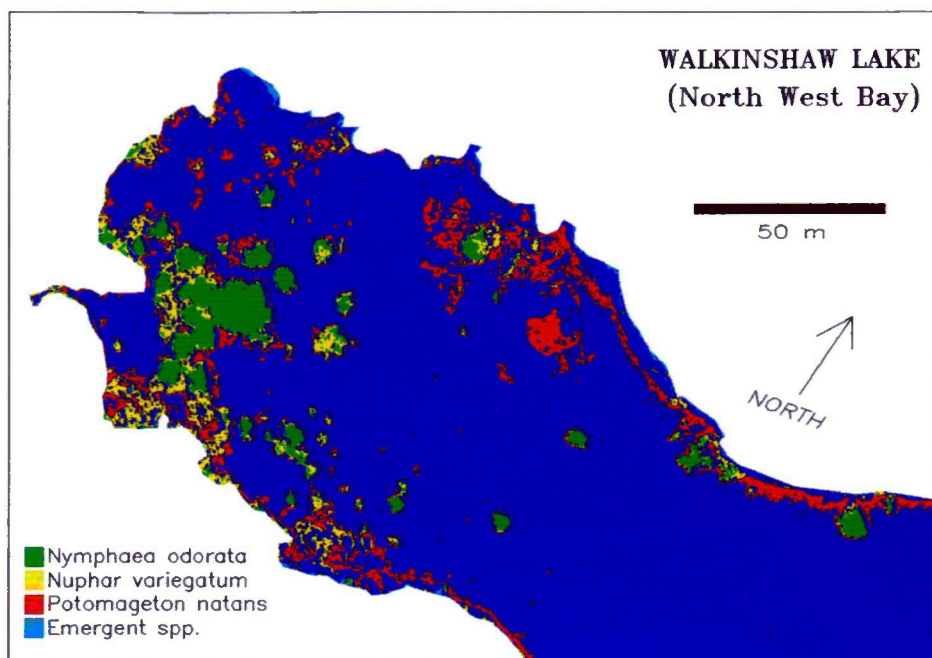


Figure 2.2 Classification map illustrating species-level differentiation of floating-leafed macrophytes within the northwest bay of Walkinshaw Lake.

revealed a high level of concordance between the true species distribution and that defined on the classification map.

Field surveys indicated that the density of vegetation, especially *N. odorata*, varied considerably from site to site. Not surprisingly, spectral signature values for this species were also found to differ on the basis of these density patterns. In its most profuse state, solid green mats are formed on the lake surface. Under more moderate growth conditions, small interstices of water appear amongst the leaves, modifying the signature value. These interstices are more common and of larger size under conditions of sparse growth, shifting the signature still. It was therefore possible to create a classification map of *N. odorata* density through analysis of this signature variation (Figure 2.3). Calibration of these classes in terms of actual biomass values has not yet been attempted, but close agreement has been noted between this classification map and *N. odorata* densities as assessed visually in the field.

As a further evaluation of the image analysis approach, a second lake with a distinctly different macrophyte community was examined. Big Pearl Lake supports vast submersed beds of *Potamogeton robbinsii*, with *Potamogeton pectinatus* and a submersed form of *Potamogeton gramineus* also occurring occasionally. Two emergent species, *Equisetum fluviatile* and *Scirpus validus*, were also very common, with *T. latifolia* occurring in occasional nearshore locations. Floating-leafed plants were a less conspicuous component of the community, comprised entirely of *P. gramineus*, *P. natans*, and *N. variegatum*.

The classification of these plants proved more difficult than with Walkinshaw Lake. Due to its highly transparent waters and shallow depth, light penetrates to the bottom throughout Big Pearl Lake, and its substrate type and zonation patterns are readily discernable on the aerial

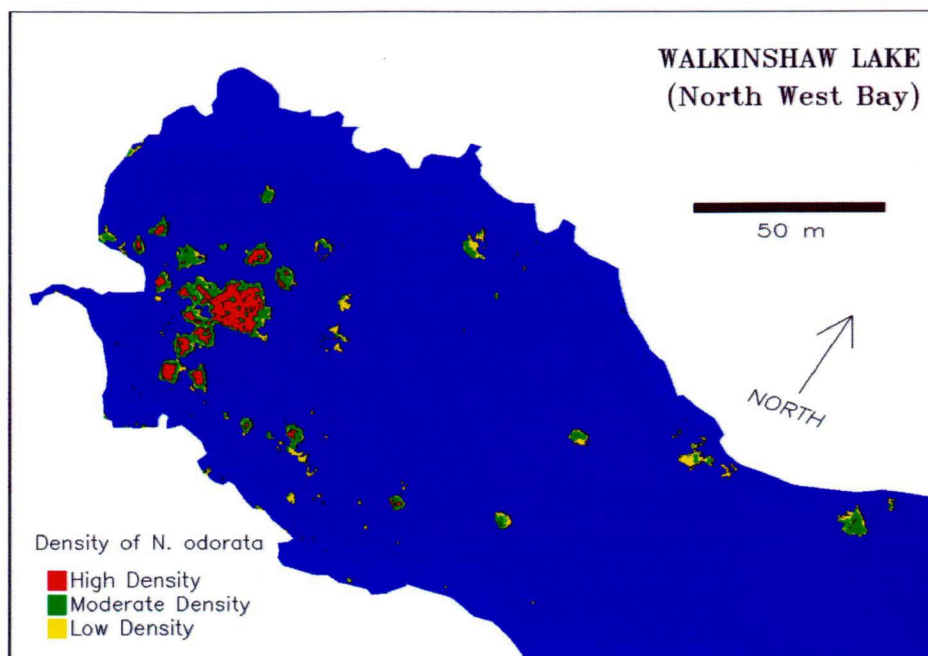


Figure 2.3 Classification map illustrating density zonation of *N. odorata* within the northwest bay of Walkinshaw Lake.

photographs. In contrast to the uniformly dark water of Walkinshaw Lake, the reflectance of light from the substrate resulted in a wide range of spectral values being recorded for the non-vegetated, open-water portion of Big Pearl Lake. Some of these values closely resembled those of the vegetation signatures, and confounded the classification process. To minimize this effect, a mask was created to block off large sections of the lake where macrophytes did not occur. Following this operation, it was possible to identify signatures representing the major plant categories, and a vegetation map for this lake was produced (Figure 2.4). The creation of this mask, however, was a time-consuming chore which demanded intimate prior knowledge of macrophyte distribution; this negated many of the gains associated with the image analysis approach.

The results of this exercise were compared with those obtained from manual photo-interpretation, and revealed quite similar areas of submersed plant cover (Table 2.4). This agreement can be attributed to the fairly regular and clearly-defined boundary associated with the *P. robbinsii* beds, which allow them to be traced with accuracy through manual means. The floating-leafed species, as with Walkinshaw Lake, were more scattered and had ill-defined boundaries. Once more, this contributed to an inflated area of plant cover when maps were produced using the visual interpretive approach.

Neither method adequately mapped the distribution of emergent plants in Big Pearl Lake. Extensive beds of *E. fluviatile* and *S. validus* were present, which are spike-like in appearance, arising from the water as erect, naked stems. While highly visible when viewed laterally, these plant colonies are difficult to discern when positioned directly overhead, especially during windless periods when they are near perpendicular to the water surface. The aerial photography was taken

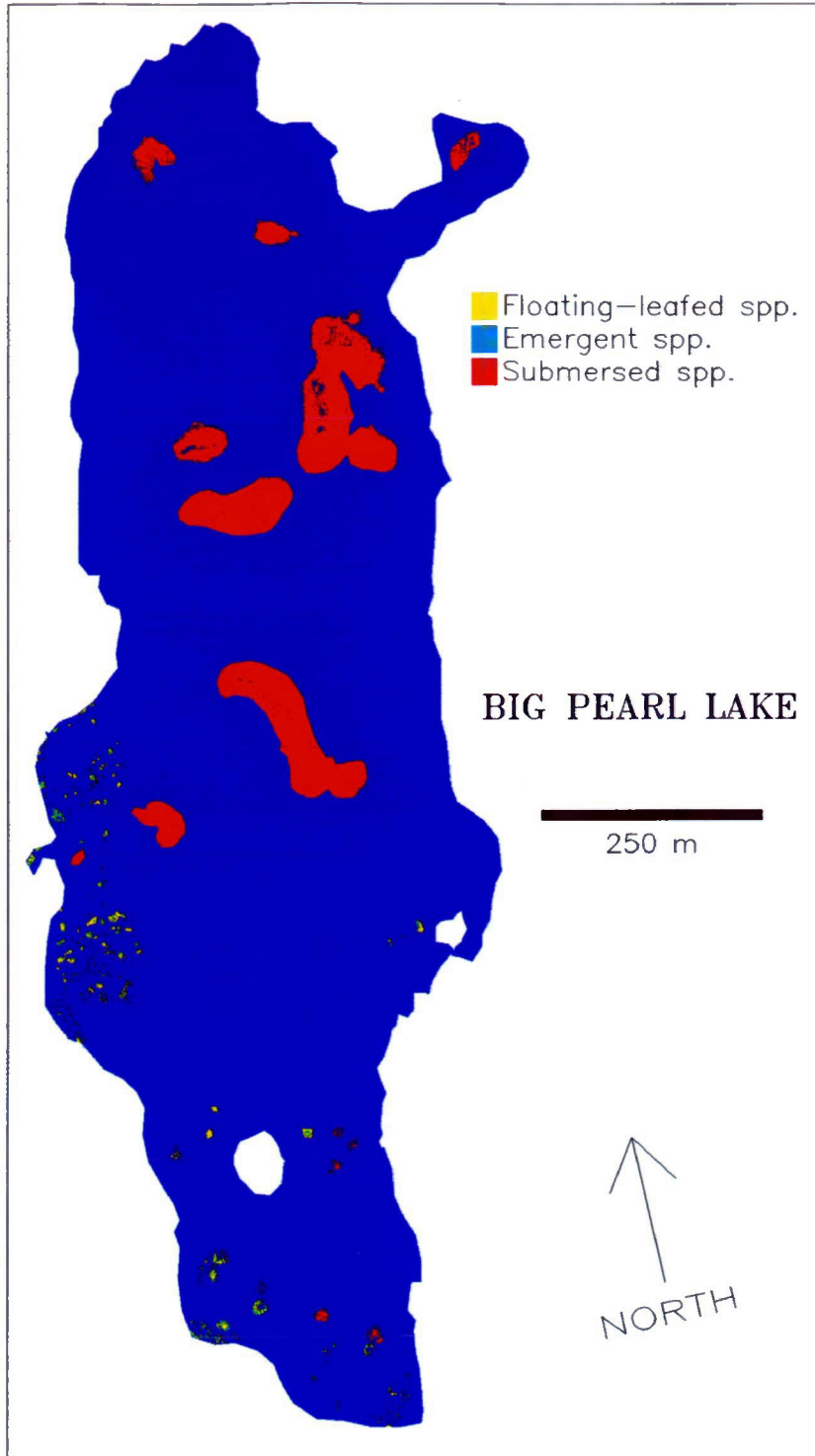


Figure 2.4 Classification map depicting the distribution of major macrophyte groups of Big Pearl Lake.

Table 2.4: A comparison of cover estimates for different macrophytes in Big Pearl Lake, determined through image analysis and the visual interpretive technique.

	% of Total Lake Area		Difference (%)
	Image Analysis Technique	Visual Interpretive Technique	
Submersed <i>spp.</i>	6.45	6.65	+ 3.1
Floating-leafed <i>spp.</i>	0.53	1.00	+ 88.7
Emergent <i>spp.</i>	0.09	0.12	+ 33.3

under such conditions, and these plants form a very indistinct image, if at all, on the photographs. In contrast, leafy emergent plants stand out clearly on the photographs and could be readily mapped using the image analysis technique.

2.5 Discussion

The mapping of macrophytes and other aquatic features using computer image analysis represents a promising new application. Maps of high accuracy and detail can be produced using this technique, especially of floating-leafed and leafy-emergent species. Once proficiency is gained with the software, it may also prove much more time efficient than the manual mapping approach. For example, the entire classification procedure for Walkinshaw lake, beginning with the mosaicking and scanning of photographs and ending with the printing of the vegetation maps, was accomplished by one person in a single day.

This technique, however, is not without its drawbacks. Although it was possible to define a robust set of signature values for broad vegetation classes (e.g. large-leafed floating plants) which could be applied across all lakes, species-level signatures were not fully transportable to other lakes. Effects such as the developmental stage of the plants, differences in the clarity and colour reproduction of the aerial photographs, and environmental influences such as sun angle, haze, and wave glitter together act to subtly alter the spectral reflectance patterns of plants from lake to lake. It would appear that for differentiation at the species level, a custom set of signatures may have to be defined for each lake. Submersed species represent another problem area, with water colour and substrate reflection affecting the classification performance.

Another drawback is the steep learning curve associated with the currently available slate of image analysis software. It is expected that the 'user friendliness' will improve as these products gain

in popularity and become more widely distributed. Even so, for proper application of this technique at least a basic knowledge of image analysis theory is required. There are many considerations and variations in methods which may influence the success of the operation, such as scanning density, photographic scale, image enhancement, and classification method (Jensen 1986).

As scan densities increase, an improvement in classification and mapping accuracy might be expected. A degree of compromise is required, however, as the digital image files quadruple in size with a doubling in the scan density. A 10 cm by 20 cm colour image, for example, would require 1.5 MBytes of storage space if scanned at a density of 50 pixels·cm⁻¹; the same image would require 24.0 MBytes of storage if scanned at 200 pixels·cm⁻¹. Similarly, an increase in the photographic scale would improve map resolution, but also at the expense of image size. Large images tax computer resources, both in terms of storage capacity and processing time, and some trade-offs must be made.

Experimentation with supervised and unsupervised classification methods demonstrated that useful results could be obtained using either procedure. However, the process of selecting representative training sites and performing the subsequent signature evaluation, as required by the supervised method, proved to be a fairly time-consuming process. Repeated selection of training samples and manipulation of signature values were required to ensure their robustness. In contrast, the interpretation of plant classes could be carried out rapidly when applying the unsupervised sequential clustering method, and became the method of choice during these trials. It is quite possible, though, that better classification methods may exist for this application, as there are a vast variety of image enhancement algorithms and clustering methods which were not fully investigated as part of this exercise.

It must be emphasized that this approach does not negate the need for ground surveys. An exception would be the simple broad classification of floating-leafed or emergent vegetation, which could be accomplished without any visit to the field due to the distinctness of their signature values. For more detailed mapping, some prior knowledge of plant distribution is required, regardless of which classification method is selected. However, for simple distributional studies, field sampling effort can be substantially reduced. An initial visual scan of the photographs will reveal contrasting vegetation patches, and the species composition of each can be determined through selective field sampling of representative patches. With this limited knowledge, aquatic vegetation maps and GIS overlays of the entire lake can be readily generated. Density mapping of certain taxa is an added benefit of this approach, which could lead to a refinement in stratified survey designs for macrophyte production studies.

3. An inexpensive sampler for the rapid quantitative collection of rooted aquatic macrophytes

3.1 Abstract

A sampling device for macrophytes has been developed which has many advantages over traditional sampling gear. It provides a 'plug' of rooted plants of known area, which can be collected rapidly across a wide range of water depth. The device is inexpensive to manufacture, is lightweight and easily transported, and requires a single person to operate. The sampler is effective for all rooted aquatic plants, with the exception of very small submersed varieties, and some extremely large and robust emergent forms. It functions well on hard substrate, such as gravel, sand, and clay, where dredges and similar sampling gear are inefficient. Details on the design, operation, and performance of the sampler are documented.

3.2 Introduction

The quantitative sampling of aquatic macrophytes can be a difficult, costly, and time-consuming process. An unbiased estimation of plant biomass demands that all plants be sampled along a series of line transects, or within a number of randomly-chosen quadrats (Gertz 1984; Raschke and Rusanowski 1984). The number of sampling units required is often substantial, depending on the variability and distribution of plant types, the size of the sampling units, and the precision of the estimate required (Green 1979; Nichols 1984).

Divers are frequently employed to directly remove plants at the required sampling location; alternatively, plants are collected indirectly by employing various mechanical sampling devices (Wetzel 1964; Westlake 1969). The use of divers offers the advantage of precise removal by hand of all plants, regardless of size, kind, and substrate type, from within both shallow and deep water sampling frames. Their effectiveness is reduced in turbid waters, however, and even under optimal conditions this is an exceedingly time-consuming process, and relatively few samples can be collected in a given sampling period.

Remote sampling devices, such as corers, scoops, and dredges, can be employed from small boats, and speed the collection process considerably. These devices, however, were initially designed to sample bottom fauna and substrate materials, and are not optimized for the collection of aquatic plants. Their inadequacies as plant samplers include small sample areas, the wrongful inclusion and exclusion of plants at the edges, and their inability to operate satisfactorily on hard lake bottoms (Westlake 1969; Raschke and Rusanowski 1984). Several customized macrophyte samplers have been developed to overcome these problems (Forsberg 1959; Brown 1984; Osborne 1984; Sabol 1984; Sliger et al. 1990), but these are generally massive and complicated devices which require permanent platforms with booms, winches, or pumps.

None of these methods or devices are entirely suited for the rapid sampling of aquatic plants for biomass studies, especially when numerous lakes are involved, and lake access is limited. A sampling device was therefore developed to meet the following criteria: 1) be capable of producing a quantifiable sample of rooted macrophytes without the need of a diver's assistance; 2) be inexpensive to manufacture; 3) be lightweight and easily transported from site to site; 4) be rapidly deployed by a single operator; and 5) be functional at both shallow and deep water sites, in clear or turbid water.

This paper describes the design and function of a macrophyte sampler which meets these specifications. The performance of this device is documented in relation to a variety of plant species and different substrate types.

3.3 Methods

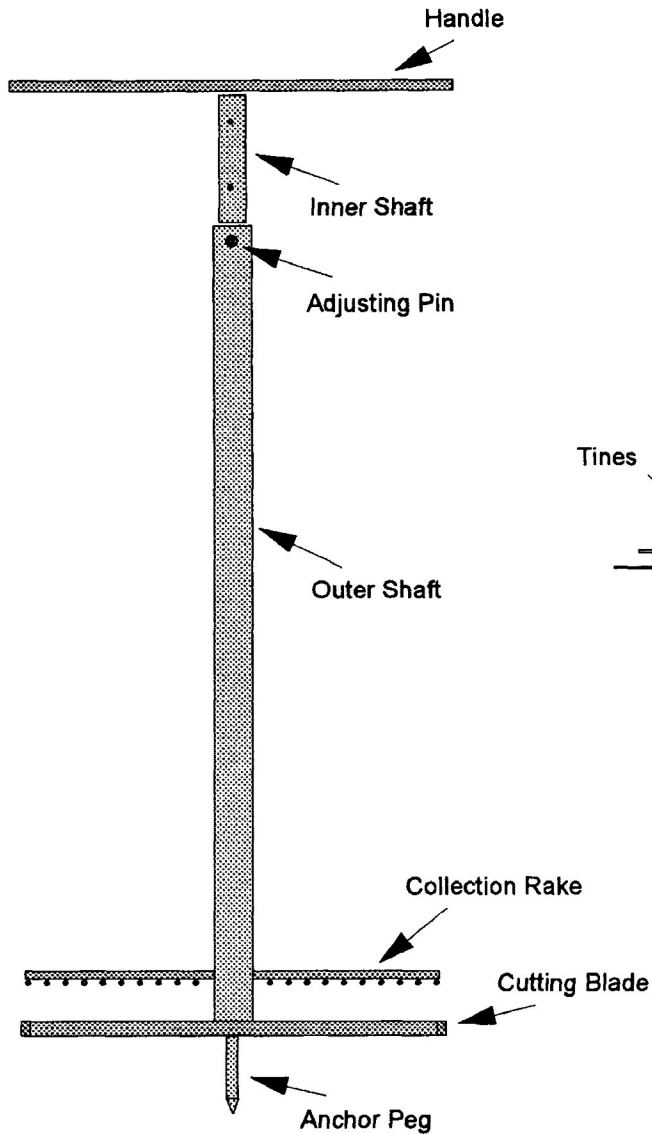
3.3.1 Construction Design

A simple design was adopted, with a cutting blade employed to shear off plant stems at the substrate surface, and a lateral rake-like structure positioned to entangle the freed vegetation and allow its retrieval to the surface. The sampler incorporates no moving parts, and to ensure a light weight (2.1 kg) is manufactured entirely of aluminum, with the exception of its steel cutting blade and collection rake.

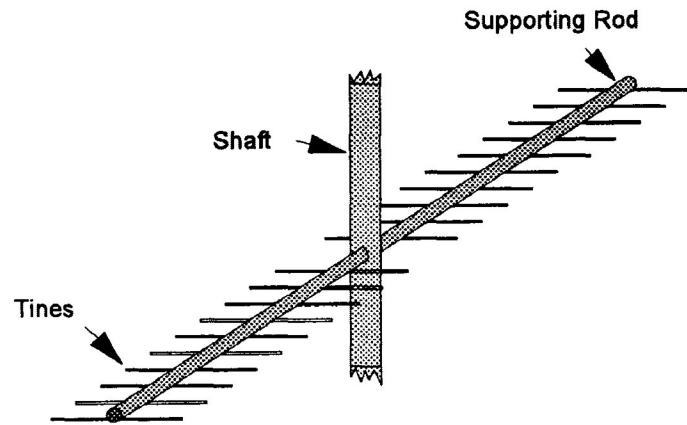
The sampler consists of a hollow vertical shaft 2.8 cm in diameter and 135 cm in length, within which slides a second solid shaft 2.5 cm in diameter and 125 cm in length (Figure 3.1(A)). The inner shaft is drilled with a series of holes at 10 cm intervals. A quick-release pin near the top of the outer shaft can be removed to allow the inner shaft to be adjusted up or down to suit the sampling depth (maximum 2.6 m). The pin is then re-fitted through the appropriate hole to securely fix the shaft.

A horizontal rod 1.6 cm in diameter and 50 cm in length is attached to the top of the inner shaft and functions as the handle, allowing the device to be rotated. A cutting blade is fitted horizontally to the bottom of the outer shaft. A 10 cm length of 0.8 cm diameter round rod, sharpened to a spear point, is threaded into the centre of the shaft below the cutting blade to

A. Plant Sampler
(Side View)



C. Collection Rake



B. Cutting Blade

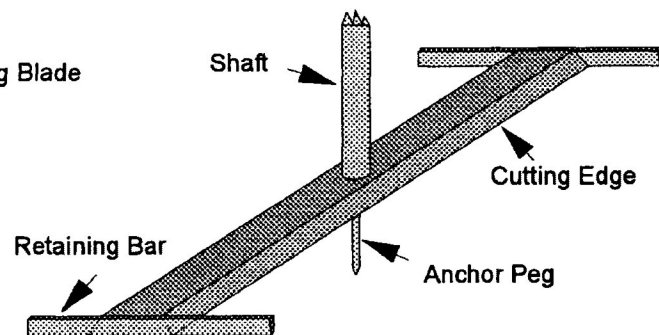


Figure 3.1 Schematic diagrams of (A) the entire sampler, in side view; (B) the cutting blade, in oblique view; and (C) the collection rake, in oblique view. The drawings are not to scale; see text for measurements of the individual components.

anchor the sampler and minimize lateral movement during rotation. A longer anchor peg (e.g. 25 cm) may be beneficial if loose sediments are commonly encountered.

The cutting blade consists of a bar of hardened steel 0.4 cm in thickness and 2.5 cm in width, bevelled and sharpened to a knife edge (Figure 3.1(B)). The length of the blade on the prototype was 45.7 cm, which provides a sample of plants from a circular quadrat of 0.164 m² in area. The length of the cutting blade could be adjusted to allow the removal of a more standard-sized sample. For example, a blade length of 50.46 cm would sample an area of .20 m², while a length of 56.42 cm would sample an area of .25 m².

To ensure that plant stems do not slip off the edge of the blade uncut, retaining bars of dimensions 0.4 cm by 1.0 cm by 10 cm are welded to the outer ends of the blade. As the device is rotated, these retaining bars determine whether plants along the outer edge will be positioned against the blade or excluded, and thus define the true outer margin of the sampling circle. The ends of these bars are bent inward slightly, to ensure that the distance between their opposing tips at either end of the blade is identical to that of the blade's length, and the desired quadrat diameter is maintained.

A structure resembling a double-sided rake is positioned 4.5 cm above the cutting blade to entangle the severed vegetation (Figure 3.1(C)). It consists of a round supporting rod, 1.0 cm in diameter, and of similar length as the cutting blade. To this rod are welded the 'tines', which are 14.5 cm lengths of 0.3 cm diameter round rod, spaced 2.0 cm apart. The addition of a second collection rake, may be advantageous in entangling certain types of vegetation. It would be of similar construction to the first, but fitted with a sliding collar to allow it to be positioned at different heights along the shaft.

3.3.2 Operation of Sampler

While grasping the handles in an upright position, the sampler is thrust to the lake bottom, and the anchor peg pressed firmly into the substrate until the cutting blade rests on the sediment surface. Taking care to maintain a strict vertical position, the sampler is then rotated in either a clockwise or counter-clockwise direction. A rotation of 180° will sever the stems of firmly attached plants from their root systems, or free the roots of those weakly attached from the sediments.

The rotation of the sampler should continue for at least one entire revolution. This ensures that the severed or freed plants become firmly entangled in the collection rake and along the shaft of the sampler. The device is then withdrawn and the plants removed. Care should be taken to lift the sampler vertically through the water column following the same path through which it was dropped. The sample obtained represents a circular core or 'plug' of vegetation of known diameter, from which plant biomass can be estimated on an areal basis.

The sampler can be utilized by a single operator wading in shallow waters, or working from a sampling platform (i.e. boat or canoe). If a platform is used, it must be maintained in a fairly stationary position throughout the sampling operation, to minimize lateral movement which could alter the quadrat size and introduce sampling error.

3.4 Results and Discussion

3.4.1 Plant Selectivity

The device is effective as a sampler of rooted macrophytes which have stems or leaves of sufficient length (approximately 8 cm, or greater) to ensure entanglement in the collection rake.

Through underwater observations, an assessment was made of the relative efficiency of the sampler's operation with different classes of aquatic plants (Table 3.1).

The sampler proved very effective for all floating-leaved plants encountered, for all submersed species except the very smallest forms, and for all emergent plants of short to medium length. Members of these groups have stems which shear off cleanly above the roots, or else their roots pull free from the sediments as they become entangled around the shaft and within the collection rake. The loss of vegetation was rarely observed, with the exception of senescent plant material which is torn apart by the mechanical action of the sampler.

Difficulties were encountered with two classes of plants. Very small submersed varieties which embrace the bottom (e.g. *Isoetes macrospora*) were generally uprooted rather than cut by the blade. While this is not considered a problem, the short stem and leaves of these species do not readily entangle in the rake, and few are retrieved by the sampler. If these types of plants are abundant and important to the study, the use of a dredge or grab sampler would be better suited for their collection.

A second difficult group of plants to sample consisted of the very large emergent forms, with robust stems comprised of layers of overlapping leaves (e.g. *Typha latifolia*, *Scirpus acutus*, *Phragmites maximus*). Repeated blows were required to sever the stems of these plants, which could shift the anchor point of the sampler. In addition, these are erect, rigid forms, which do not entangle well on the collection rake; frequently some of the severed plant leaves were released by the sampler and floated freely to the surface. This group of plants favours shallow water, and it is suggested that when encountered they instead be removed by hand from an established quadrat.

Table 3.1: Performance appraisal of sampler on different categories of rooted aquatic vegetation.

Macrophyte Category	Representative Taxa	Observed Performance of Sampler
Emergent, tall, single slender stems	<i>Equisitum fluviatile</i> <i>Eleocharis palustris</i>	Good - stems shear cleanly above roots - very rigid stems entangle poorly, with slight loss encountered
Emergent, tall, stems dense and robust	<i>Typha latifolia</i> <i>Scirpus acutus</i>	Fair - stems difficult to shear - variable entanglement on sampler, with some loss observed
Emergent, medium or short varieties	<i>Sagittaria latifolia</i> <i>Hypericum ellipticum</i>	Excellent - stems shear above roots or roots pull free - plants entangle readily on sampler; all retained
Floating-leaved, all types	<i>Nymphaea odorata</i> <i>Potamogeton natans</i>	Excellent - stems shear cleanly above roots - all plants entangle and are retained by sampler
Submersed, tall or medium forms	<i>Potamogeton richardsonii</i> <i>Myriophyllum heterophyllum</i>	Excellent - stems shear cleanly above roots - all plants entangle and are retained by sampler
Submersed, very small varieties	<i>Isoetes macrospora</i> <i>Carex lasiocarpa</i>	Poor - stems do not shear; plants may be displaced from sediments - few plants entangle for retrieval

Care must also be exercised when sampling the more slender, tall, emergent plants, such as *Eleocharis palustris*. While their stems shear easily and cleanly above the roots, their rigidity is such that they may entangle poorly in the sampler. The loss observed from the sampler was slight, but must be acknowledged. A second collection rake positioned further up the shaft may help prevent this loss.

3.4.2 Substrate Considerations

Aquatic plants grow on a variety of substrate, ranging from the interstices of boulders and rubble to expanses of soft organic matter. The performance of different sampling devices is strongly linked to the substrate present when carrying out the sampling trials.

In general, this sampler functions best on hard bottoms, such as gravel, sand, or clay (Table 3.2). It performs equally well where thin to moderate layers of silt or detritus are present, and the anchor peg can penetrate into the hard substrate below. On these surfaces, the sampler can be firmly placed and pivoted on its anchor peg with the absence of noticeable lateral drift. Plants growing on hard substrate are usually firmly attached, and this facilitates a clean severing of their stems by the cutting blade. Other common sampling devices, such as dredges and corers, perform quite poorly under these conditions (e.g. gravel, detritus).

A decline in the sampler's performance is noticeable when applied within areas of deep organic muck or marl, or where silt and detritus occur in exceptionally deep layers. Under these conditions, the anchor point is unstable, and lateral movement can occur and generate sampling error. This problem may be alleviated somewhat by replacing the anchor peg with one of longer length. A second concern is that some plants grow totally submersed within marl or organic materials (e.g. *Nitella flexilis*), or root at varying depths within them. In these circumstances,

Table 3.2: Performance appraisal of sampler on different substrate types.

Substrate Type	Observed Performance of Sampler
Rock, rubble	<p>Poor</p> <ul style="list-style-type: none"> - anchor point cannot be maintained on solid surface - uneven surface restricts blade rotation
Gravel, sand	<p>Excellent</p> <ul style="list-style-type: none"> - anchor point easily maintained - stems severed readily by blade
Clay	<p>Excellent</p> <ul style="list-style-type: none"> - anchor point easily maintained - stems severed readily by blade
Silt, detritus	<p>Good to excellent</p> <ul style="list-style-type: none"> - anchor point easily maintained except where material occurs in exceptionally thick layers - stems severed readily by blade or roots freed
Organic muck	<p>Fair</p> <ul style="list-style-type: none"> - anchor point difficult to maintain as material normally occurs in thick layers - roots usually pulled free from loose sediments

rather than resting the cutting blade on a hard substrate, it must be suspended at some predetermined depth within the loose sediment. This procedure is difficult to follow, especially under conditions where the sampler's position in the substrate cannot be observed.

The sampler performs poorly in areas where rubble and larger rock material are predominant, as do most other sampling devices. It is difficult or impossible to establish a firm anchor point except in the rock interstices, which may not correspond with the centre of the sampling quadrat. In addition, the uneven surface may not provide adequate clearance for the blade to rotate. Plant density is usually low in such areas, however, and hand removal may be the best option for collection in these instances.

3.4.3 Water Depth, Transparency, and Currents

The transparency of the water does not impede the sampler's performance; unlike that of a diver, it is normally unnecessary to view the bottom while collecting the sample. Similarly, water depth does not affect its operation, and samples can be collected to a maximum depth of 2.6 m. If samples are required beyond this depth, the adjustable shafts could be lengthened to accommodate these circumstances.

A known bias in deep-water sampling relates to water currents. In areas where flowing water positions large submersed plants at an angle to the surface, the sampler, upon its descent or retrieval, can snag and collect plants which are rooted outside the sampling quadrat. This problem also plagues other plant samplers and dredges, and there are no obvious solutions, other than determining the extent of the bias and applying subsequent corrective measures.

General Summary and Conclusions

This thesis documents progress in three areas: 1) the development of Carlson-style trophic status models for lakes of northwestern Ontario, adjusted for water colour and macrophyte abundance; 2) the use of digital image analysis of aerial photographs as a means of accurately mapping macrophyte distribution; and 3) the design of a sampling device which provides a rapid and inexpensive means of collecting quantitative samples of aquatic macrophytes .

The relationships between Secchi disk transparency, total phosphorus concentration, and chlorophyll *a* concentration for a continental lake set were used by Carlson (1977) to develop the Trophic State Index (TSI). It was found that for lakes of northwestern Ontario, different relationships exist between these variables than those documented by Carlson, with more light attenuation and less chlorophyll production per unit phosphorus. On the basis of these differences, the TSI was recalibrated to be applicable to lakes of the Laurentian Precambrian Shield. It was found that the inclusion of a corrective term for water colour and aquatic macrophyte abundance explained significantly more of the variance between the trophic parameters. The TSI models were further modified to include these corrective terms, and an improvement in their performance was noted when the standing stock of benthos was used as a response variable.

Digital image analysis of aerial photographs is offered as an alternative to the visual interpretive technique for mapping the distribution of aquatic macrophytes. Some disadvantages have been documented, such as the difficulty in classifying certain submergent vegetation, the inability to transport species-level signatures over space and time, and the steep learning curve associated with image analysis software. However, once proficiency is gained in the use of the software, this

technique becomes very time-efficient. Other advantages are obvious, such as the ability to produce highly accurate classification maps of floating-leafed and leafy emergent vegetation. Differentiation to species is possible for some forms, and in certain instances, it may be possible to further differentiate these species into density classes. Map resolution may be radically improved through this approach, with the edge detail of plant beds very highly defined. This, in turn, contributes to a more accurate estimation of total plant coverage and biomass.

Finally, a sampling device has been developed which has many advantages over traditional sampling gear. It is lightweight, and easily transported and operated by a single person. It can be used in water depths ranging to 2.6 m, and is particularly valuable when used on hard substrates, where dredges and other sampling gear are particularly inefficient. It is an effective tool for the quantitative sampling of all rooted aquatic plants, with the exception of very small submersed varieties and some extremely large and robust emergent forms.

References

- Aizaki, M., A. Otsuki, T. Fukushima, M. Hosomi, and K. Muraoka. 1981. Application of Carlson's trophic state index to Japanese lakes and relationships between the index and other parameters. *Verh. Internat. Verein. Limnol.* 21: 675-681.
- Andrews, D.S., D.H. Webb, and A.L. Bates. 1984. The use of aerial remote sensing in quantifying submersed aquatic macrophytes. p. 92-99. [In] W.M. Dennis and B.G. Isom(eds.) *Ecological Assessment of Macrophyton: Collection, Use, and Meaning of Data*, ASTM STP 843, Philadelphia, PA.
- Aronoff, S. 1989. *Geographic information systems: A management perspective*. WDL Publications, Ottawa, Can. 294 p.
- Armstrong, F.A.J., and D.W. Schindler. 1971. Preliminary chemical characterization of waters in the Experimental Lakes Area, northwestern Ontario. *J. Fish. Res. Board Can.* 28: 171-187.
- Balls, H., B. Moss, and K. Irvine. 1985. The effects of high nutrient loading on interactions between aquatic plants and phytoplankton. *Verh. Internat. Verein. Limnol.* 22: 2912-2915.
- Best, M.D., and K.E. Mantai. 1978. Growth of *Myriophyllum*: sediment or lake water as the source of nitrogen and phosphorus. *Ecology* 59: 1075-1080.

- Bogucki, D.J., and G.K. Gruending. 1978. Remote sensing to identify, assess, and predict ecological impact on Lake Champlain wetlands. Final Report of Project C-6075, Office of Water Research and Technology, Washington, D.C. 191 p.
- Brezonik, P.L. 1978. Effect of organic colour and turbidity on Secchi disk transparency. *J. Fish. Res. Board Can.* 35: 1410-1416.
- Brook, A.J. 1965. Planktonic algae as indicators of lake types, with special reference to the *Desmidiaceae*. *Limnol. Oceanogr.* 10: 403-411.
- Brown, C. 1984. Improved above-substrate sampler for macrophytes and phytomacrofauna. *Prog. Fish Cult.* 46(2): 142-144.
- Canfield, D.E., Jr. 1983. Prediction of chlorophyll (a) concentrations in Florida lakes: The importance of phosphorous and nitrogen. *Water Res. Bull.* 19(2): 255-262.
- Canfield, D.E. Jr., and L.M. Hodgson. 1983. Prediction of Secchi disc depths in Florida lakes: Impact of algal biomass and organic color. *Hydrobiologia* 99: 51-60.
- Canfield, D.E. Jr., M.V. Hoyer, and C.M. Duarte. 1990. An empirical method for characterizing standing crops of aquatic vegetation. *J. Aquat. Plant Manag.* 28: 64-69.
- Canfield, D.E. Jr., K.A. Langeland, 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.

- 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(2): 361-369.
- Carter, V., and N. B. Rybicki. 1990. Light attenuation and submersed macrophyte distribution in the tidal Potomac River and estuary. *Estuaries* 13(4): 441-452.
- Chambers, P.A., E.E. Prepas, M.L. Bothwell, and H.R. Hamilton. 1989. Roots versus shoots in nutrient uptake by aquatic macrophytes in flowing waters. *Can. J. Fish. Aquat. Sci.* 46: 435-439.
- Chiandani, G., and M. Vighi. 1974. The N:P ratio and tests with *Selenastrum* to predict eutrophication in lakes. *Water Res.* 8: 1063-1069.
- Chilton, E.W. 1990. Macroinvertebrate communities associated with three aquatic macrophytes (*Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Vallisneria americana*) in Lake Onalaska, Wisconsin. *J. Freshw. Ecol.* 5(4): 455-466.
- Chow-Fraser, P., and H.C. Duthie. 1983. An interpretation of phosphorus loadings in dystrophic lakes. *Arch. Hydrobiol.* 97(1): 109-121.
- Crawford, S.A. 1979. Farm pond restoration using *Chara vulgaris* vegetation. *Hydrobiologia* 62: 17-31.

- Cullis, K.I. 1986. Standing stock estimates of benthic fauna for a lake set in Northwestern Ontario. Ont. Fish. Tech. Rep. Ser. No. 21: iii & 20 p.
- Dermott, R.M., J. Kalff, W.C. Leggett, and J. Spence. 1977. Production of *Chironomus*, *Procladius*, and *Chaoborus* at different levels of phytoplankton biomass in Lake Memphemagog, Quebec-Vermont. J. Fish. Res. Board Can. 34: 2001-2007.
- Dillon, P.J., and F.H. Rigler. 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. J. Fish. Res. Board Can. 31(11): 1771-1778.
- Duarte, C.M. 1987. Use of echosounder tracings to estimate the aboveground biomass of submerged plants in lakes. Can. J. Fish. Aquat. Sci. 44: 732-735.
- Duarte, C.M., J. Kalff, and R.H. Peters. 1986. Patterns in biomass and cover of aquatic macrophytes in lakes. Can. J. Fish. Aquat. Sci. 43: 1900-1908.
- Evans, M.S. 1990. Large-lake responses to declines in the abundance of a major fish planktivore - the Lake Michigan example. Can. J. Fish. Aquat. Sci. 47: 1738-1754.
- Fee, E.J., R.E. Hecky, M.P. Stainton, P. Sandberg, L.L. Hendzel, S.J. Guildford, H.J. Kling, G.K. McCullough, C. Anema, and A. Salki. 1989. Lake variability and climate research in Northwestern Ontario: study design and 1985-1986 data from the Red Lake District. Can. Tech. Rep. Fish. Aquat. Sci. 1662: v & 39 p.
- Forsberg, C. 1959. Quantitative sampling of subaquatic vegetation. Oikos 10(II): 233-240.

- Forsgren, P., and M. Wallsten. 1987. Computer aided interactive classification and mapping of aquatic areas. *Int. Revue Ges. Hydrobiol.* 72: 257-262.
- Gasaway, R.D., and T.F. Drda. 1978. Effect of grass carp introduction on macrophytic vegetation and chlorophyll content of phytoplankton in four Florida lakes. *Florida Sci.* 41: 101-109.
- Gertz, S.M. 1984. Biostatistical aspects of macrophyton sampling. p. 28-35. [In] W.M. Dennis and B.G. Isom (eds.) *Ecological Assessment of Macrophyton: Collection, Use and Meaning of Data*, ASTM STP 843, Philadelphia, PA.
- Green, R.H. 1979. *Sampling design and statistical methods for environmental biologists*. John Wiley and Sons, New York. 257 p.
- Haegeler, C.W., and M.J. Hamey. 1980. Shoreline vegetation on herring spawning grounds in Barkley Sound in 1978 compared with similar assessments for 1974 and 1975. *Fish. Mar. Serv. MS Rep.* 1549. 37 p.
- Hanson, J.M. 1990. Macroinvertebrate size-distributions of two contrasting freshwater macrophyte communities. *Freshwat. Biol.* 24: 481-491.
- Hanson, J.M., and R.H. Peters. 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. *Can. J. Fish. Aquat. Sci.* 41: 439-445.
- Hassler, A.D., and E. Jones. 1949. Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. *Ecology* 30: 359-364.

- Hern, S.C., V.W. Lambou, L.R. Williams, and W.D. Taylor. 1981. Modifications of models predicting trophic state of lakes: adjustment of models to account for the biological manifestations of nutrients. U.S. Env. Monitoring Systems Lab. Las Vegas, Nevada. 38 p.
- Hutchinson, G.E. 1938. On the relation between the oxygen deficit and the productivity and typology of lakes. *Int. Rev. Gesamten Hydrobiol. Hydrogr.* 36: 336-355.
- Jarnefelt, H. 1952. Limnological classification of lakes. *Fennia* 72: 202-208.
- Jeffries, D.S., F.P. Dieken, and D.E. Jones. 1977. Evaluation of the autoclave digestion method for total phosphorus analysis. Laboratory Services Branch, Ontario Ministry of the Environment, Rexdale, Ontario. 18 p.
- Jensen, J.R. 1986. *Introductory digital image processing: A remote sensing perspective.* Prentice-Hall, Englewood Cliffs, New Jersey. 379 p.
- Jones, J.R., and R.W. Bachmann. 1976. Prediction of phosphorus and chlorophyll levels in lakes. *J. Water Pollution Contr. Fed.* 48(9): 2176-2182.
- Jones, R.C. 1990. The effect of submersed aquatic vegetation on phytoplankton and water quality in the tidal freshwater Potomac River. *J. Freshwater Ecol.* 5: 279-287.
- Kitchell, J.F., M.S. Evans, D. Scavia, and L.B. Crowder. 1988. Regulation of water quality in Lake Michigan: report of the food web workshop. *J. Great Lakes Res.* 14: 109-114.

- Koenings, J.P., and J.A. Edmundson. 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: effects of yellow color and turbidity. *Limnol. Oceanogr.* 36: 91-105.
- Lasenby, D.C. 1975. Development of oxygen deficits in 14 southern Ontario lakes. *Limnol. Oceanogr.* 20: 993-999.
- Macomber, R.T., and G.H. Fenwick. 1979. Aerial photography and seaplane reconnaissance to produce the first total distribution inventory of submersed aquatic vegetation in Chesapeake Bay, Maryland. p. 498-503, In: *Proceedings of the American Society of Photogrammetry. Volume II. 45th Annual Meeting, March 18-24, 1979, Washington, D.C.*
- Matuszek, J.E. 1978. Empirical predictions of fish yields of large North American lakes. *Trans. Am. Fish. Soc.* 107: 385-394.
- McCauley, E., J. A. Downing, and S. Watson. 1989. Sigmoid relationships between nutrients and chlorophyll among lakes. *Can. J. Fish. Aquat. Sci.* 46: 1171-1175.
- Mitchell, S.F. 1989. Primary production in a shallow eutrophic lake dominated alternatively by phytoplankton and submerged macrophytes. *Aquat. Bot.* 33: 101-110.
- Nicholls, K.H., and P.J. Dillon. 1978. An evaluation of phosphorus-chlorophyll-phytoplankton relationships for lakes. *Int. Revue Ges. Hydrobiol.* 63(2): 141-154.

- Nichols, S.A. 1984. Quantitative methods for assessing macrophyte vegetation. p. 7-15. [In] W.M. Dennis and B.G. Isom (eds.) Ecological Assessment of Macrophyton: Collection, Use, and Meaning of Data, ASTM STP 843, Philadelphia, PA.
- Olson, D.P. 1964. The use of aerial photographs in studies of marsh vegetation. Bulletin 13, Tech. Series. Maine Agricultural Experiment Station. 62 p.
- Ontario Ministry of the Environment. 1981. Outlines of analytical methods. Laboratory Services Branch, Ontario Ministry of the Environment, Rexdale, Ontario. 269 p.
- Osborne, J.A. 1984. The Osborne submersed aquatic plant sampler for obtaining biomass measurements. p. 58-68. [In] W.M. Dennis and B.G. Isom (eds.) Ecological Assessment of Macrophyton: Collection, Use, and Meaning of Data, ASTM STP 843, Philadelphia, PA.
- Osgood, R.A. 1982. Using differences among Carlson's trophic state index values in regional water quality assessment. Water Res. Bull. 18(1): 67-74.
- Pace, M.L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus-chlorophyll *a* relationship. Can J. Fish. Aquat. Sci. 41: 1089-1096.
- Phillips, G.L., D. Eminson, and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. Aquat. Bot. 4: 103-126.
- Plante, C., and J.A. Downing. 1989. Production of freshwater invertebrate populations in lakes. Can. J. Fish. Aquat. Sci. 46: 1489-1498.

- Porcella, D.B., S.A. Peterson, and D.P. Larsen. 1979. Proposed method for evaluating the effects of restoring lakes. p. 265-310. [In] *Limnological and Socioeconomic Evaluation of Lake Restoration Projects: Approaches and Preliminary Results*. U.S. Environmental Protection Agency.
- Prairie, Y.T., C.M. Duarte, and J. Kalff. 1989. Unifying nutrient-chlorophyll relationships in lakes. *Can. J. Fish. Aquat. Sci.* 46: 1176-1182.
- Raschke, R.L., and P.C. Rusanowski. 1984. Aquatic macrophyton field collection methods and laboratory analyses. p. 16-27. [In] W.M. Dennis and B.G. Isom (eds.) *Ecological Assessment of Macrophyton: Collection, Use, and Meaning of Data*, ASTM STP 843, Philadelphia, PA.
- Rasmussen, J.B., L. Godbout, and M. Schallenberg. 1989. The humic content of lake water and its relationship to watershed and lake morphometry. *Limnol. Oceanogr.* 34: 1336-1343.
- Rasmussen, J.B., and J. Kalff. 1987. Empirical models for zoobenthic biomass in lakes. *Can. J. Fish. Aquat. Sci.* 44: 990-1001.
- Ryan, P.A. 1980. An analysis of the factors affecting the phytoplankton standing crop and potential fish yield of West Patricia lakes. *West Patricia Land Use Plan. Fisheries Technical Report #7*. Ontario Ministry of Natural Resources. 58 p. & Appendices

- Sabol, B.M. 1984. Development and use of the waterways experiment station's hydraulically operated submersed aquatic plant sampler. p. 46-57. [In] W.M. Dennis and B.G. Isom (eds.) Ecological Assessment of Macrophyton: Collection, Use and Meaning of Data, ASTM STP 843, Philadelphia, PA.
- Sakamoto, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. Arch. Hydrobiol. 62(1): 1-28.
- Sand-Jensen, K., and M. Sondergaard. 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. Int. Revue Ges. Hydrobiol. 66: 529-552.
- SAS Institute Inc. 1987. SAS/STAT Guide for Personal Computers, Version 6 Edition. SAS Institute Inc., Cary, NC. 1028 p.
- Savino, J.F., and R.A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Trans. Am. Fish. Soc. 111: 255-266.
- Savino, J.F., and R.A. Stein. 1989. Behavioural interactions between fish predators and their prey: effects of plant density. Anim. Behav. 37: 311-321.
- Schloesser, D.W., C.L. Brown, and B.A. Manny. 1988. Use of aerial photography to inventory aquatic vegetation. J. Aerosp. Eng. 1(3): 142-150.

- Schloesser, D.A., and B.A. Manny. 1984. Rapid qualitative method for estimating the biomass of submersed macrophytes in large water bodies. *J. Aquat. Plant Manage.* 22: 102-104.
- Schloesser, D.W., B.A. Manny, C.L. Brown, and E. Jaworski. 1987. Use of low-altitude aerial photography to identify submersed aquatic macrophytes. *Color Aerial Photography in the Plant Sciences and Related Fields: Proc. of 10th(1985) Biennial Workshop, Univ. Michigan, Ann Arbor.* p. 19-28.
- Schramm, H.L., and K.J. Jirka. 1989. Epiphytic macroinvertebrates as a food resource for bluegills in Florida lakes. *Trans. Amer. Fish. Soc.* 118: 416-426.
- Shapiro, J. 1977. The current status of lake trophic indices - A review. North American Project - A Study of US Water Bodies. A Report for the OECD. United States Environmental Protection Agency, Corvallis, Oregon.
- Sliger, W.A., J.W. Henson, and R.C. Shadden. 1990. A quantitative sampler for biomass estimates of aquatic macrophytes. *J. Aquat. Plant Manag.* 28: 100-102.
- Timms, R.M. and B. Moss. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol. Oceanogr.* 29: 472-486.
- Titus, J.E., and M.S. Adams. 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. *Oecologia* 40: 273-286.

- Tyler, J.E. 1968. The secchi disc. *Limnol. Oceanogr.* 13(1): 1-6.
- Vollenweider, R.A. 1968. The scientific basis of lake and stream eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Tech. Rep. DAS/DSI/68.27 OECD, Paris.
- Walker, W.W. Jr. 1979. Use of hypolimnetic oxygen depletion rate as a trophic state index for lakes. *Int. Revue Ges. Hydrobiol.* 15(6): 1463-1470.
- Watkins, C.E., J.V. Shireman, and W.T. Haller. 1983. The influence of aquatic vegetation upon zooplankton and benthic macroinvertebrates in Orange Lake, Florida. *J. Aquat. Plant Manag.* 21: 78-83.
- Watson, S., E. McCauley, and J.A. Downing. 1992. Sigmoid relationships between phosphorus, algal biomass, and algal community structure. *Can. J. Fish. Aquat. Sci.* 49: 2605-2610.
- Welch, R. 1989. Desktop mapping with personal computers. *Photogramm. Eng. Remote Sens.* 55(11): 1651-1662.
- Westlake, D.F. 1964. Light extinction, standing crop and photosynthesis within weed beds. *Verh. Int. Verein. Limnol.* 15: 415-425.

- Westlake, D.F. 1969. Sampling techniques and methods for estimating quantity and quality of biomass. *Macrophytes*. p. 25-40. [In] R.A. Vollenweider (ed.) IBP Handbook No. 12: A manual on methods for measuring primary production in aquatic environments. Blackwell Scientific Publications, Oxford.
- Wetzel, R.G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large, shallow lake. *Int. Revue Ges. Hydrobiol.* 49(1): 1-61.
- Wetzel, R.G. 1990. Land-water interfaces: Metabolic and limnological regulators. *Verh. Internat. Verein. Limnol.* 24: 6-24.
- Wetzel, R.G., and B.A. Manny. 1972. Secretion of dissolved organic carbon and nitrogen by aquatic macrophytes. *Verh. Int. Verein. Limnol.* 18: 162-170.
- Wium-Andersen, S., U. Anthoni, C. Christophersen, and G. Houen. 1982. Allelopathic effects on phytoplankton by substances isolated from aquatic macrophytes (*Charales*). *Oikos* 9: 187-190.