Use of the Morphoedaphic Index to Predict Nutrient Status and Algal Biomass in Some Canadian Lakes

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The underlying assumptions of the morphoedaphic index (MEI; total dissolved solids (TDS)/mean depth), which has been used to predict fish yields in lakes, and its power for predicting biomass at lower trophic levels were examined using published data. The assumptions included the relationship between mean depth of lakes and various hydrologic characteristics (flushing rate and stratification regime), water transparency characteristics (water color and turbidity), and the stoichiometric relationship among ions (expressed as a proportion between TDS and the concentration of primary nutrients, total phosphorus (TP) and total nitrogen (TN)). Although these basic assumptions could be supported empirically, the predictive power of the MEI became progressively weakened with increasing trophic level. MEI accounted for up to 85% of the variation in TP and TN, less than 50% of the variation in [Chl *a*], and none of the variation in the biomass of herbivorous zooplankton. The functions relating TDS to both TP and TN were fundamentally different: as lakes increased in salinity, the TN:TP ratio decreased dramatically so that TP almost exceeded TN concentrations in extremely saline lakes. This necessitated the development of separate MEI–nutrient relationships for saline (TDS > 1000 mg/L) and nonsaline lakes.

Au moyen de résultats qui ont paru, nous avons examiné les hypothèses qui sous-tendent l'utilisation de l'indice morphoédaphique (IME; matières totales dissoutes/profondeur moyenne), indice qui a servi à prévoir le rendement des lacs en poisson; nous avons examiné aussi l'efficacité de cet indice comme moyen de prévision de la biomasse à des niveaux trophiques inférieurs. Les hypothèses considérées portent notamment sur les rapports entre la profondeur moyenne des lacs et différentes caractéristiques hydrologiques (vitesse de renouvellement de l'eau et régime de stratification), la transparence de l'eau (couleur de l'eau et turbidité) ainsi que les proportions stochiométriques entre les différents ions (exprimées en rapport entre les matières totales dissoutes et la concentration des éléments nutritifs primaires, du phosphore total (PT) et de l'azote total (NT)). Quoique ces hypothèses fondamentales trouvaient une justification empirique, il demeure que la capacité de prévision de l'IME s'affaiblit progressivement à mesure qu'on progresse dans l'échelle trophique. L'IME permettait de justifier jusqu'à 85 % des variations de PT et de NT, il permettait de justifier moins de 50 % des variations de la concentration en chlorophylle *a*, et il ne permettait de justifier aucunement les variations de la biomasse du zooplancton herbivore. Les fonctions qui établissaient une relation entre les matières totales dissoutes et le PT ainsi que le NT étaient fondamentalement différentes : à mesure qu'on progressait dans l'échelle de salinité des lacs, le rapport NT:PT diminuait de manière spectaculaire, au point que la concentration en PT dépassait presque la concentration en NT dans les lacs extrêmement salés. Il a donc fallu développer des fonctions distinctes pour mettre en relation l'IME et les éléments nutritifs dans les lacs salés (matières totales dissoutes supérieures à 1 000 mg/L) qui sont distinctes de celles des lacs non salés.

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The morphoedaphic index (MEI; Ryder 1965), calculated as the concentration of total dissolved solids ([TDS]) divided by mean depth, is commonly used by fisheries biologists to predict potential fish yield in lakes (Ryder et al. 1974; Matuszek 1978; Kerr 1982). Although the original MEI was derived empirically (Ryder et al. 1974; Ryder 1982), the conceptual framework that underlies this model include the following explicit assumptions: (1) bedrock geology and climate largely determine the [TDS] entering lakes, and TDS is a surrogate for essential nutrients such as phosphorus and nitrogen which control the lake's primary productivity; and (2) mean depth, an overall parameter of lake morphometry, affects the distribution of organisms and is a surrogate for hydrological characteristics such as stratification (temperature regime), nutrient circulation, and dilution, all of which affect how energy is processed within the water column (i.e. mean depth is representative of a nutrient and energy sink in lakes; Rawson 1951, 1952; Northcote and Larkin 1956; Ryder 1965; Hanson and Leggett 1982).

In the two and a half decades since its introduction, the MEI has been used widely in fisheries management through appropriate modifications accounting for regional and global climatic differences (Henderson et al. 1973; Ryder et al. 1974; Schlesinger and Regier 1982) and modifications accounting for differences in hydraulic retention time and ionic composition of lake water (Jenkins 1982). Recently, its usefulness in aquatic sciences has been under scrutiny. On technical grounds, criticisms include the inaccurate prediction limits around estimates due to artificial correlation between dependent and independent variables in the model (Schneider and Haedrich 1989) and the biased nature of ratios due to spurious correlations and the use of inappropriate null models (Jackson et al. 1990). Other crit-

TABLE 1. Range and mean values (±SE) corresponding to studies assembled for this investigation. Mean values are in parentheses. TP = [total phosphorus] (μg/L); TN = [total nitrogen] (μg/L); CHL = [Chl *a*] (μ/L); n/a = not available.

Location	Investigators and study	No. of lakes	TP	TN	CHL	Mean depth (m)
British Columbia coast	Shortreed and Stockner 1981; Stockner et al. 1980	21	3.0–18.0 (5.2±3.1)	118–208 (158±28.5)	0.8–2.0 (1.3±0.5)	13–212 (55.2±51.8)
	Stockner and Shortreed 1985	4	1.0–4.0 (1.9±1.4)	120–126 n/a	0.7–3.3 (1.5±1.2)	39–59 (46.0±15.8)
Central Alberta	Chow-Fraser and Trew 1990	16	14.0–66.0 (30.9±16.4)	546–1666 (1077±300.5)	2.6–25.0 (10.2±7.5)	2.9–53.0 (11.5±12.4)
	Prepas and Trew 1983[a]	17	11.0–152.0 (46.8±34.7)	495–4104 (1669±1088)	1.7–80.6 (23.7±21.4)	3.2–19.4 (8.2±5.0)
	Bierhuizen and Prepas 1985	20	21–14077 (2215±4158)	1094–10736 (4781±2274)	3.5–90.0 (26.2±30.4)	0.9–8.0 (3.6±2.1)
Nova Scotia	Kerekes 1975	20	2.8–10.9 (7.4±2.9)	n/a	0.3–2.9 (1.7±0.7)	1.4–74.0 (6.6±16.0)
Quebec	Pace 1984	12	3.4–55.7 (13.0±13.9)	n/a	1.2–28.6 (5.3±7.5)	2.9–44.0 (17.8±14.3)
	Chow-Fraser and Maly 1991	8	13.4–47.2 (28.7±12.4)	n/a	2.3–8.95 (4.8±2.5)	n/a
	Bird and Kalff 1984[b]	2	10.0	n/a	4.0–4.6	n/a
	Chow-Fraser and Duthie 1987	4	6.7–19.6	n/a	1.3–2.1	n/a
Ontario	Zimmerman et al. 1983	37	3.0–18.0 (7.7±3.9)	203–673 (350±94)	0.3–7.5 (2.2±1.5)	0.9–20.1 (7.6±4.3)

[a] Excludes lakes included in Chow-Fraser and Trew (1990) and Bierhuizen and Prepas (1985).

[b] Only one value of TP available.

TABLE 2. Summary of Pearson correlation coefficients (see Methods for explanation of abbreviations and units). Only significant correlation coefficients are reported. $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; $^{****}P < 0.0001$. All values were log-transformed except pH.

	Mean depth	Max depth	*A*	FR	TURB	COLOR	TDS	COND
Max depth	+0.91****							
A	+0.45****							
FR	−0.49****	−0.53****	−0.37**					
TURB			+0.63****					
COLOR	−0.59****				+0.69***			
TDS	−0.79****			−0.63****	−0.32**	+0.46**		
COND	−0.43****	−0.25*			−0.36*		+0.99****	
pH	−0.46****	−0.26*		−0.50**	−0.48**		+0.90****	+0.90****

icisms concern the ineffectiveness of the MEI to predict fish production when compared with other indices based on surface area (Youngs and Heimbuch 1982) or lake productivity indicators (Hanson and Leggett 1982; Prepas 1983; Downing et al. 1990).

Since one of the basic assumptions of the MEI is the presumed proportionality between TDS and primary nutrients (based on the stoichiometric relationship among ions in lake water), it is surprising that in some lakes, nutrient concentration could accurately predict yield/production when the MEI could not. To understand how the MEI fails to predict fish yield in these situations, there must be a better understanding of the general relationship between MEI and the concentrations of primary nutrients (i.e. total phosphorus (TP) and total nitrogen (TN)). It is also important to investigate the effectiveness of the MEI for predicting biomass at lower trophic levels, since primary productivity was a good predictor of fish yield in some lakes (Downing et al. 1990).

In this paper, I have assembled data from the literature to first examine the two basic assumptions of the MEI: the stoichiometric relationship between TDS and primary nutrients and the relationship between mean depth and variables that may affect lake productivity such as hydrologic characteristics and water transparency. I have purposely included lakes that cover a large geographical area to test the general effectiveness of the MEI for predicting nutrient concentration in a wide range of lake types. Although all study lakes occur in Canada, I have included lakes from the United States in an independent lake set to test the general applicability of relationships that emerge from this study. Secondly, I examine the relationship between MEI and plankton biomass to evaluate the general applicability of the MEI for predicting energy flow at lower trophic levels. By testing these underlying assumptions, I hope to provide a better understanding of the nature and source of disparities between the MEI and biomass at higher trophic levels.

Methods

I have focused on Canadian lakes in this paper primarily to minimize the effect of large-scale climatic variations on the

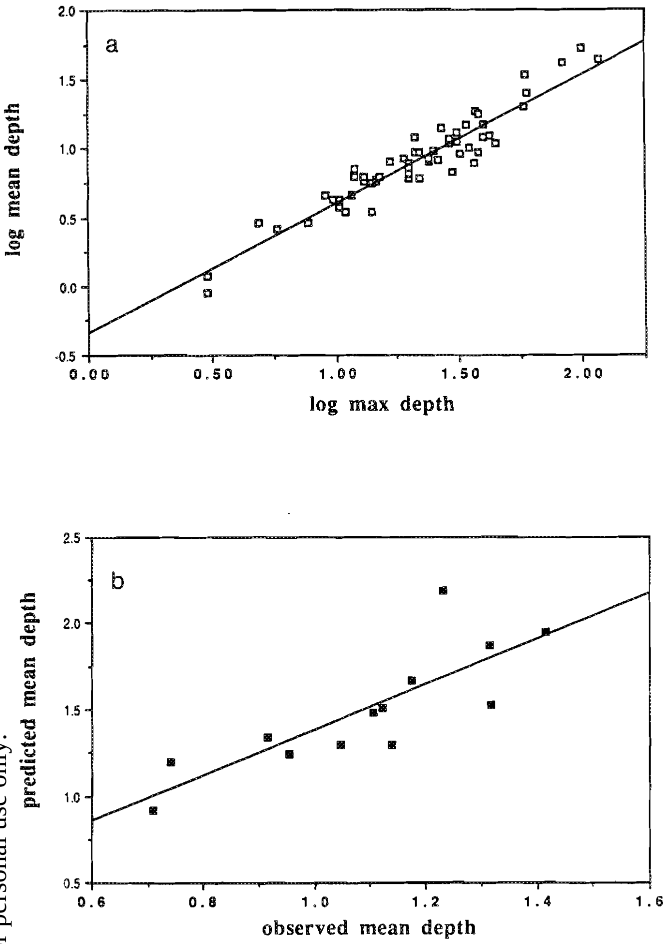

FIG. 1. (a) Log mean depth (m) versus log maximum depth (m) for study lakes. Equation for least-squares regression line is log mean depth = 0.940 (± 0.058) log max depth −0.349 (r^2 = 0.82; n = 60; P = 0.0001). (b) Predicted versus observed mean depth (m) from Rawson's (1960) study. The line indicates that predicted = observed.

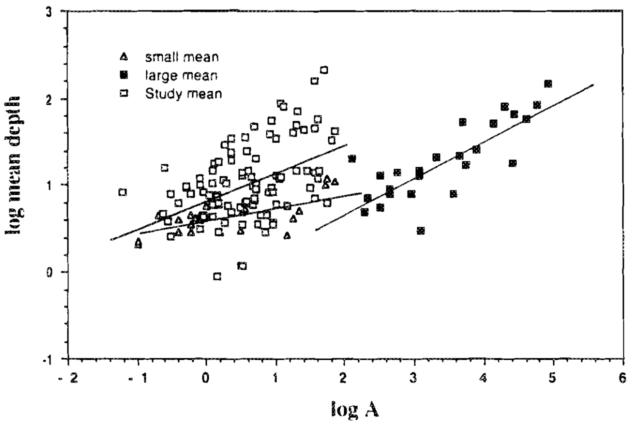

FIG. 2. Log mean depth (m) versus log lake surface area (A; km^2). Open symbols are data for small lakes ($A \leq 100$ km^2) and closed symbols are those for large lakes ($A > 100$ km^2). Open squares are data from this study; closed squares and open triangles are those from the independent dataset (see Methods). Equation for regression line through open squares is log mean depth = 0.312 (± 0.058) log A + 0.768 (r^2 = 0.20; n = 119; P = 0.0001). Equation for regression line through open triangles is log mean depth = 0.161 (± 0.033) log A + 0.597 (r^2 = 0.50; n = 26; P = 0.0001). Equation for regression line through closed squares is log mean depth = 0.413 (± 0.064) log A −0.135 (r^2 = 0.65; n = 25; P = 0.0001).

TABLE 3. Mean depth (m) associated with stratification characteristics of study lakes. All categories are significantly different from each other as indicated by an ANOVA and multiple range test ($P < 0.05$).

Mixing regime	n	Mean depth	SE
Nonstratified	53	3.06	1.14
Weakly stratified	28	10.81	1.18
Stratified	47	19.36	1.10

MEI (Schlesinger and Regier 1982); however, I have relaxed all restrictions pertaining to basin size, lake depth and elevation, salinity, turbidity, and flushing rate. The 161 lakes included in the study are located throughout Canada from Nova Scotia to British Columbia (Table 1). Not all of these lakes were included in every analysis because some variables were not measured or were not made available. Compared with other published studies in which the MEI has been evaluated (e.g. Ryder 1965; Matuszek 1978; Jones and Hoyer 1982; Prepas 1983), this study contains a wide range of values.

Variables Included

As mean depth (metres) is only one of several morphometric parameters, I included maximum depth (max depth; metres) and lake surface area (A; square kilometres) in my analysis. I chose flushing rate (FR; per year) and the lake's stratification characteristic (STRAT) as the main hydrologic parameters because they are readily reported and both play a role in dilution and regeneration of nutrients in the water column (Murphy 1962; Kerekes 1973; Nurnberg and Peters 1984). As a measure of reduced water transparency resulting from nonalgal sources, I chose turbidity (TURB; JTU) and color (Pt units), which are both implicated in suppressing primary productivity (Murphy 1962; Janus and Vollenweider 1981; Hoyer and Jones 1983).

Because TDS (milligrams per litre) was not always available, I also used specific conductance (COND; microsiemens per centimetre)) in the numerator of the MEI because the latter is widely used as a measure of mineral salt concentration and is well correlated with TDS (Bayly and Williams 1973; Foster et al. 1981). pH was also included in my analysis because it can be used as a surrogate of TDS and COND when neither is available (r = + 0.90 for both variables; Table 2). The two primary nutrients included were TP (micrograms per litre) and TN (micrograms per litre) whereas biotic variables included [Chl a] (CHL; micrograms per litre) and the biomass of phytoplankton (PHYTO; micrograms per litre) and herbivorous zooplankton (HERB; micrograms per litre). Lakes designated as saline in this study are those of Bierhuizen and Prepas (1985) who described these lakes as having high TDS (values >1000 mg/L) with high salt concentration rather than humic substances.

Independent Data Set

To test the generality of empirical relationships obtained in this study, I assembled values from previously published studies on morphoedaphic factors and fish yield to form an independent data set. The data set included TP, CHL, COND, mean depth, and A from Jones and Hoyer (1982), mean depth and A

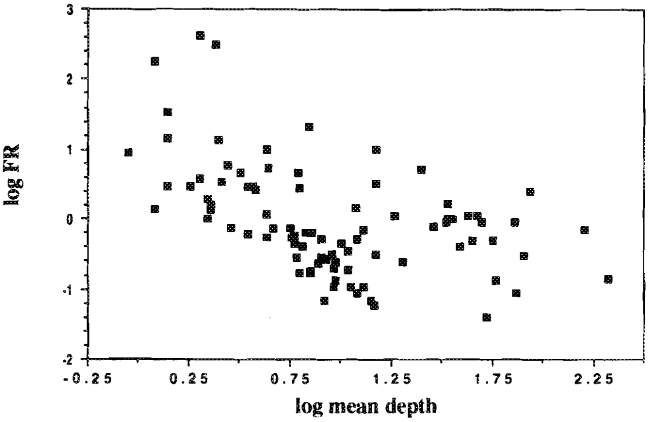

FIG. 3. Log flushing rate (FR) versus log mean depth (m).

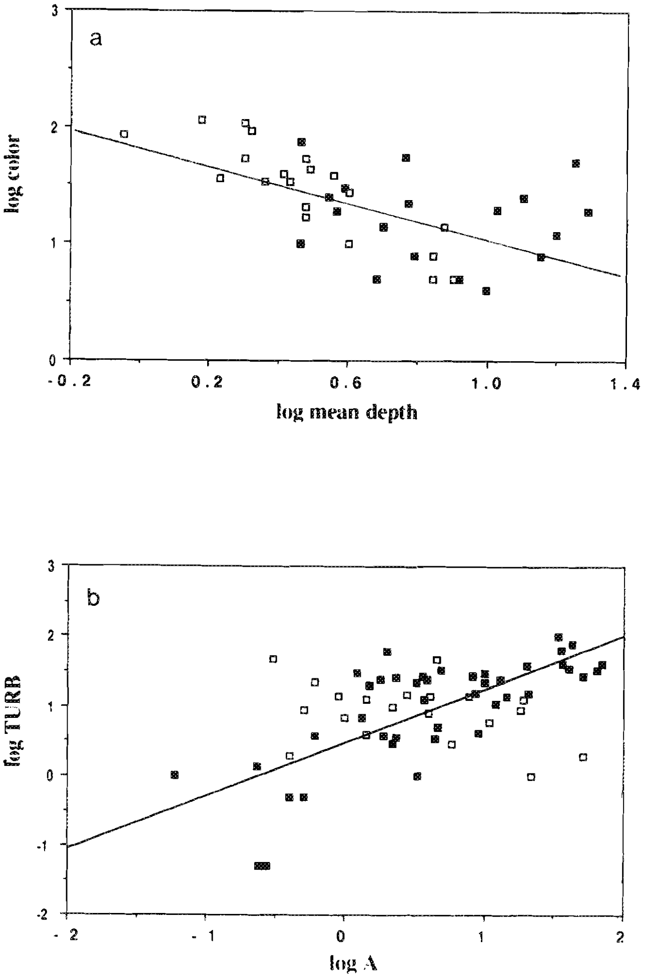

FIG. 4. (a) Log color versus log mean depth (m). Open symbols correspond to saline lakes and closed symbols correspond to nonsaline lakes (TDS $>$ and $\leq$ 1000 mg/L, respectively). Equation for regression through both open and closed symbols is log color = -0.778 ($\pm$ 0.174) log mean depth + 1.845 ($r^2 = 0.35$; $n = 39$; $P = 0.0001$). (b) Log turbidity (TURB; JTU) versus log surface area (A; km^2). Key for symbols are as in Fig. 4a. Equation for regression through both open and closed symbols is log TURB = 0.607 ($\pm$ 0.096) log A + 0.600 ($r^2 = 0.40$; $n = 62$; $P = 0.0001$).

from Youngs and Heimbuch (1982), TDS from Ryder (1965) and Matuszek (1978), and mean depth, max depth, STRAT, and the biomass of netplankton (kilograms dry weight per hectare) from Rawson (1960).

Statistical Treatment

All of the data except pH and STRAT were first $\log_{10}$-transformed (referred to as log in the remainder of the text) to stabilize the variance and normalize the residuals. Linear and multiple regression analyses were performed and, where appropriate, subsequent analysis of covariance was carried out (Sokal and Rohlf 1981). In all cases, the criterion level for significance was 0.05.

Results and Discussion

Testing the Assumptions of the MEI

Although mean depth is the variable Ryder (1965) used in his original formulation of the MEI, other morphometric variables may also be used. Youngs and Heimbuch (1982), for example, suggested that mean depth was only a surrogate of lake surface area (A), and that A should instead be used. This conclusion was recently reinforced by studies on Finnish lakes (Ranta and Lindstrom 1989, 1990). The deepest spot in the lake (max depth) may also be used as a surrogate if the relationship between mean and maximum depth is known. I found a highly significant correlation between mean depth and max depth (Fig. 1a). The good predictive power of this regression model was demonstrated when I tested it using independent data from Rawson's (1960) study (Fig. 1b). The good fit of values to the line of unity indicates that max depth may in general be a good substitute for mean depth and that an alternative MEI may be calculated with either max depth or values estimated from max depth.

By comparison, the relationship between mean depth and A was more complex. The regression in this case only explained 20% of the overall variability in mean depth, and the equation only seemed to apply to small lakes ($\leq$100 km^2; open symbols in Fig. 2). This was obvious when I plotted values from the independent data set (see Methods; closed squares and open triangles) together with those in the study (open squares). The study data overlapped completely with those of small lakes (open triangles) but did not at all overlap with those of large lakes (closed squares). Slopes of the regression lines through study data and that through large lakes in the independent data set were not significantly different ($P > 0.05$); an analysis of covariance further indicated that their intercepts were significantly different ($P < 0.05$). Because A was only correlated with mean depth for lakes within respective size categories, it is doubtful that Youngs and Heimbuch's (1982) proposal to use A as a surrogate of mean depth can be generally applied without some qualifications.

Morphometry versus hydrology

There was an apparent relationship between mixing regime of lakes and their mean depth (Table 3). On average, nonstratified lakes were shallow (1–8 m) whereas strongly stratified lakes were deep (4–200 m), while weakly stratified lakes were intermediate in depth (5–158 m). Average mean depths of nonstratified systems was only 3.1 m, compared with 19.4 m for stratified lakes. Therefore, mean depth appears to be a rough indicator of the mixing regime in lakes.

TABLE 4. Summary of significant regression equations between TP and TN and some other variables. SE = standard error of the regression coefficient.

Y variable	*X* variable	*n*	r^2	*P*	*b*	SE	*a*
log TP	log max depth	65	0.29	0.0001	−0.491	0.097	1.732
log TP	log mean depth	129	0.27	0.0001	−0.812	0.120	1.965
log TN		97	0.39	0.0001	−0.712	0.092	3.499
log TP	log COLOR	48	0.17	0.0042	0.794	0.265	0.851
log TN		36	0.46	0.0001	0.583	0.109	2.653
log TP	log TDS	77	0.81	0.0001	1.012	0.056	−0.875
log TN		63	0.76	0.0001	0.603	0.043	1.556
log TP	log COND	78	0.68	0.0001	0.850	0.066	−0.509
log TN		71	0.83	0.0001	0.545	0.030	1.607
log TP	pH	102	0.50	0.0001	0.455	0.045	−2.067

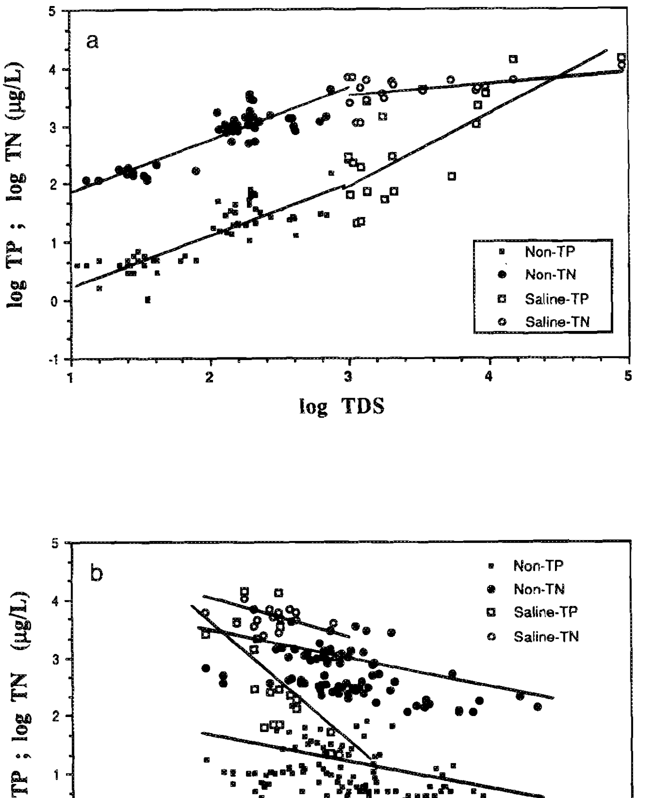

FIG. 5. Nutrient concentration versus (a) TDS for both saline and nonsaline lakes and (b) log mean depth (m). (a) Equations for nonsaline lakes are log TN = 0.862 (± 0.077) log TDS + 1.025 ($r^2 = 0.75$; $n = 43$; $P = 0.0001$) and log TP = 0.905 (± 0.081) log TDS − 0.669 ($r^2 = 0.69$; $n = 57$; $P = 0.0001$). Equations for saline lakes are log TN = 0.210 (± 0.103) log TDS + 2.899 ($r^2 = 0.19$; $n = 20$; $P = 0.05$) and log TP = 1.221 (± 0.271) log TDS − 1.584 ($r^2 = 0.53$; $n = 20$; $P = 0.0003$). (b) Equations for nonsaline lakes are log TN = −0.402 (± 0.087) log z_x + 3.073 ($r^2 = 0.22$; $n = 77$; $P = 0.0001$) and log TP = −0.368 (± 0.074) log z_x + 1.34 ($r^2 = 0.19$; $n = 109$; $P = 0.0001$). Equations for saline lakes are log TN = −0.584 (± 0.195) log z_x + 3.903 ($r^2 = 0.33$; $n = 20$; $P = 0.008$) and log TP = −2.067 (± 0.671) log z_x + 3.615 ($r^2 = 0.35$; $n = 20$; $P = 0.006$).

FR varied inversely with all three morphometric variables, mean depth, max depth, and *A* (Table 2). Shallow, small lakes appear to have a higher FR than deep, large lakes (Fig. 3). This may be because drainage ratio (drainage area to lake area) is the chief determinant of FR (Rasmussen et al. 1989) and thus the weak correlation between FR and these morphometric variables is likely due to collinearities with drainage ratio. Another explanation may be that for any given precipitation regime, drainage area divided by lake volume defines FR. Therefore, the high correlation between area and volume will undoubtedly lead to a high correlation between drainage area and lake area. In general, FR may simply follow the allometric principles detailed by Schnieder and Haedrich (1989).

Morphometry versus water transparency

Rasmussen et al. (1989) found that most highly colored lakes were small, rapidly flushed, shallow headwater lakes with large, low-sloped catchment. In this study, color was also negatively correlated with mean depth (Fig. 4a); however, it was not significantly correlated with lake area, although this may only be a consequence of the smaller sample size in this study. By comparison, TURB was significantly correlated with *A* (Fig. 4b), but not with mean depth. Thus in this study, large lakes tended to be more turbid than small lakes, regardless of mean depth. Unfortunately, the relatively small sample size ($n = 62$) in this study precludes drawing any conclusions.

These results confirm that mean depth generally yields information regarding the mixing regime and flushing rate of lakes and thus substantiate the basic assumption that mean depth is an overall surrogate of hydrologic characteristics. In addition, mean depth also reflects water transparency, since shallow lakes tend to be more highly colored and more turbid. The significant correlation of mean depth with apparently antagonistic effects is interesting. For instance, shallow lakes may be more productive because they do not stratify and the entire water column is well lit, but this effect may be cancelled by the higher FR and more turbid water that are also associated with shallow lakes, and that may bring about reduced algal productivity. Further refinement of the relationship between mean depth and the standing stock of lake biota will probably depend on clarification of the relative importance of these factors in controlling primary productivity.

TDS/COND versus nutrients

The best predictors of TP and TN were TDS and COND, which described 81 and 83%, respectively, of the variability in nutrient concentrations (Table 4). Since the data set included some saline lakes that have extremely high TDS and COND

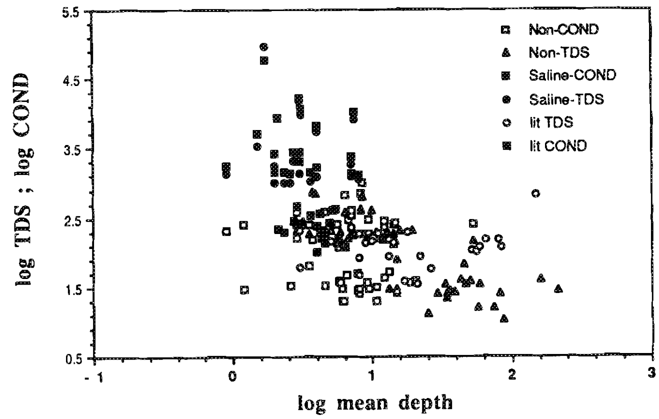

FIG. 6. Log total dissolved solids (TDS; mg/L) and log conductance (COND; μS/cm) versus log mean depth (m). Non-COND and saline-COND are conductance values for nonsaline and saline lakes, respectively; non-TDS and saline-TDS are TDS measurements for nonsaline and saline lakes, respectively; and lit-TDS and lit-COND are TDS and conductance values, respectively, for lakes in the independent data set (see Methods).

TABLE 5. Summary of significant ($\alpha = 0.05$) regression equations between TP and TN and the MEI. MEI is calculated as TDS/mean depth and MEI(C) is calculated as COND/mean depth. SE = standard error of the regression coefficient.

Y variable	*X* variable	*n*	r^2	*P*	*b*	SE	*a*
log TP	log MEI	73	0.83	0.0001	0.657	0.035	0.625
log TN	log MEI	62	0.84	0.0001	0.412	0.023	2.412
log TP	log MEI(C)	62	0.83	0.0001	0.821	0.049	0.069
log TN	log MEI(C)	68	0.83	0.0001	0.447	0.025	2.169

values (TDS values > 1000 mg/L; as defined by Bierhuizen and Prepas 1985), I was concerned that their inclusion biased the regression analysis. Therefore, I removed the saline lakes and performed the analysis again. Although the resulting r^2 values were reduced to 0.69 and 0.58, respectively, they were still substantially higher than those of any other variable tested.

When separate regression analyses were performed for saline and nonsaline lakes, I found that TN concentrations in saline lakes did not increase as quickly as TP in relation to TDS concentrations (Fig. 5a); in extremely saline lakes, TP even exceeded TN concentrations. Substitution with COND as the independent variable yielded the same trend. Thus, although TDS (or COND) is indeed a good surrogate for TP and TN in lakes, the function relating TDS to both nutrients are fundamentally different; as lakes increase in salinity, the TN:TP ratio decreases dramatically so that TN rather than TP becomes the limiting nutrient at high salinities (Rawson and Moore 1944).

Morphometry versus nutrients

Relationships between mean depth and nutrients were also influenced by lake salinity. TP concentrations corresponding to saline lakes declined sharply with lake depth (Fig. 5b) whereas those corresponding to nonsaline lakes showed a more gradual decline. By comparison, the slope of the regression between TN and depth did not differ significantly ($P > 0.05$) between lake types, although the intercepts were significantly higher ($P < 0.05$) for saline lakes. The steep slope of the regression line relating TP to depth for saline lakes suggests that the rate of enrichment in saline lakes is very rapid for lakes with shallow mean depth. This may be because accumulated TP in the sediments of saline lakes becomes more easily recirculated as lakes become more shallow. Further research should be carried out to investigate these relationships, especially since anticipated global warming may cause lake levels to drop below present levels and may trigger more problems associated with eutrophication.

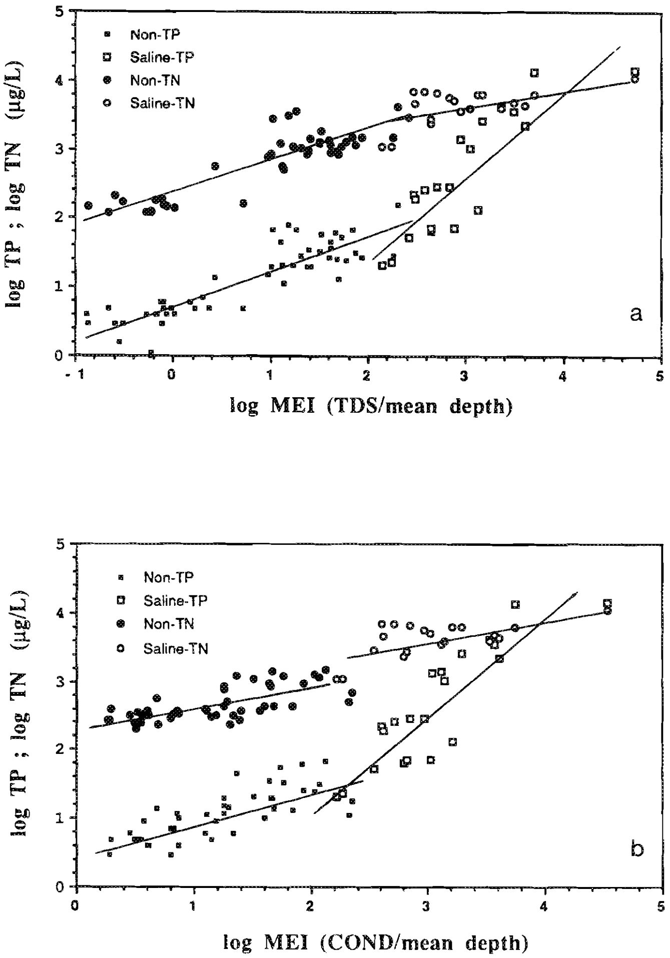

FIG. 7. Nutrient concentration versus (a) MEI (TDS/mean depth) and (b) MEI (COND/mean depth). (a) Equations for nonsaline lakes are log TN = 0.459 log MEI + 2.273 ($r^2 = 0.77$) and log TP = 0.512 log MEI + 0.716 ($r^2 = 0.77$). Equations for saline lakes are log TN = 0.253 log MEI + 2.872 ($r^2 = 0.37$) and log TP = 1.249 log MEI − 1.078 ($r^2 = 0.76$). (b) Equations for nonsaline lakes are log TN = 0.294 log MEI(C) + 2.311 ($r^2 = 0.48$) and log TP = 0.473 log MEI(C) + 0.483 ($r^2 = 0.58$). Equations for saline lakes are log TN = 0.291 log MEI(C) + 2.732 ($r^2 = 0.41$) and log TP = 1.408 log MEI(C) − 1.689 ($r^2 = 0.79$).

Test of independence between mean depth and TDS

Since collinearity between the two parameters of the MEI would decrease the predictive power of the index, I first evaluated the relationship between TDS and mean depth before proceeding with further analyses. TDS and COND (a substitute for TDS; Table 2) were both highly correlated with mean depth (Fig. 6). On closer examination, however, it was obvious that inclusion of saline lakes biased the overall trend. When I removed these data and ran the analysis again, there was no longer a significant relationship between mean depth and the

TABLE 6. Summary of significant ($\alpha = 0.05$) regression equations between CHL, PHYTO, HERB, TP, TN, and the MEI. MEI is calculated as TDS/mean depth and MEI(C) is calculated as COND/mean depth. SE = standard error of the regression coefficient.

Y variable	*X* variable	*n*	r^2	*P*	*b*	SE	*a*
log CHL	log TP	149	0.51	0.0001	0.512	0.041	−0.087
log PHYTO		52	0.17	0.0021	1.027	0.317	1.774
log HERB		43	0.14	0.0121	0.897	0.335	1.544
log CHL	log TN	91	0.66	0.0001	0.887	0.068	−1.900
log PHYTO		47	0.59	0.0001	1.943	0.241	−1.943
log HERB		41	0.45	0.0001	2.728	0.485	−4.341
log CHL	log MEI	73	0.46	0.0001	0.311	0.040	0.339
log CHL	log MEI(C)	62	0.41	0.0001	0.336	0.052	0.097
log PHYTO		36	0.29	0.0008	0.236	0.064	2.778

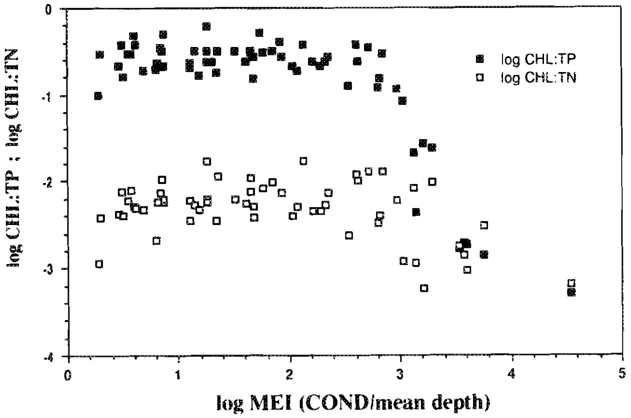

FIG. 8. Changes in CHL:TP and CHL:TN ratios with increasing MEI values.

other two variables ($P > 0.50$). This was reinforced when I superimposed literature data on the same plot and found that TDS and COND varied independently with mean depth for all non saline lakes (TDS < 1000 mg/L). This confirms the need for development of individual MEI relationships for saline and nonsaline lakes.

Relationship between MEI, Nutrients, Phytoplankton, and Zooplankton

In the previous section, I validated two assumptions of the MEI and tested the independence of the two variables in the index. I now proceed to use these variables to predict nutrient status in lakes. Since I calculated MEI using both TDS and COND in the numerator of the index, I will refer to indices calculated with TDS as MEI and those calcualted with COND as MEI(C) (Table 5). The high r^2 values indicate that both MEI and MEI(C) were good predictors of TP and TN when both saline and nonsaline lakes were included in the analysis; however, separate regressions are more ecologically meaningful for saline and nonsaline lakes because of the significant interaction between the slope of the regression and lake type (Fig. 7a and 7b). The slope for TN associated with nonsaline lakes was 0.459 whereas that for saline lakes was 0.253; by comparison, the slope for TP associated with nonsaline lakes was 0.512 whereas that for saline lakes was 1.249. Although the respective slopes could not be tested for significant differences because of non-overlapping ranges in MEI values, it is obvious that TP concentrations increased disproportionately with MEI values > 200, while corresponding TN concentrations in this range showed almost no change in slope. Similar trends were evidenced when MEI(C) was used as the independent variable. This emphasizes the need for development of separate MEI relationships for saline lakes and supports Rawson and Moore's (1944) suggestion that TN rather than TP is the limiting nutrient for primary productivity in saline systems.

TABLE 7. Summary of significant ($\alpha = 0.05$) regression equations between CHL, TP, TN, and the MEI (MEI = TDS/mean depth; MEI(C) = COND/mean depth) for nonsaline lakes only. SE = standard error of the regression coefficient.

Y variable	*X* variable	*n*	r^2	*P*	*b*	SE	*a*
log CHL	log TP	129	0.72	0.0001	0.938	0.052	−0.509
log CHL	log TN	71	0.76	0.0001	1.184	0.079	−2.658
log CHL	log MEI	53	0.68	0.0001	0.515	0.050	0.230
log CHL	log MEI(C)	42	0.47	0.0001	0.504	0.084	−0.120

MEI versus plankton biomass

CHL is routinely used as a measure of algal standing stock in pelagic ecosystems, and although it does not reflect the species composition of the phytoplankton, it is more often available in the literature than is biomass estimate from cell counts. I have included both variables in this study, but acknowledge that analyses involving phytoplankton biomass may not be as rigorous because of the much smaller sample size. Due to limited availability of zooplankton biomass data, analyses including herbivore information are likewise restricted.

Neither the MEI nor MEI(C) was as well correlated with CHL as TN or TP (Table 6). However, TP explained more residual variation than MEI ($r^2 = 0.51$ and 0.46, respectively), while TN explained the most ($r^2 = 0.66$). This is probably because saline lakes had been included in the analysis. CHL:TP ratios were greatly reduced for saline compared with nonsaline lakes whereas CHL:TN ratios did not differ greatly between lake types (Fig. 8); consequently, CHL was better correlated with changes in TN than with changes in TP when MEI values exceeded 1000. Because inclusion of saline lakes confounded the comparison, I excluded them and performed the regression analysis of the smaller data set. (I did not run new analyses for PHYTO and HERB because there were no corresponding biomass data available for saline lakes). Analysis on the reduced data set yielded identical trends (Table 7); TP and TN were still stronger predictors, and once again, TP was only marginally better than MEI ($r^2 = 0.72$ and 0.68, respectively), while TN was the best overall predictor.

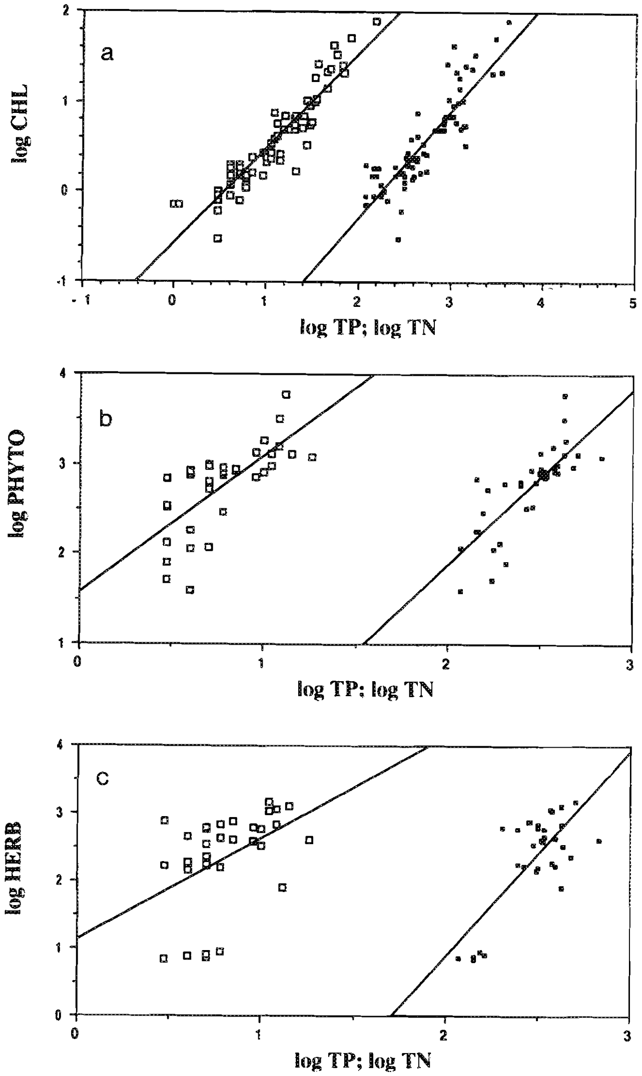

FIG. 9. (a) Log chlorophyll *a* (CHL; µg/L), (b) log phytoplankton biomass (PHYTO; µg/L), and (c) log herbivore biomass (HERB; µg/L) for nonsaline lakes in restricted lake set (see text). Equations for respective regression lines are log CHL = 1.184 (± 0.079) log TN − 2.658 (r^2 = 0.76; n = 71), log CHL = 1.051 (± 0.050) log TP − 0.567 (r^2 = 0.87; n = 71), log PHYTO = 1.943 (± 0.255) log TN − 1.994 (r^2 = 0.62; n = 38), log PHYTO = 1.518 (± 0.252) log TP − 1.585 (r^2 = 0.50; n = 38), log HERB = 3.038 (± 0.486) log TN − 5.189 (r^2 = 0.57; n = 32), and log HERB = 1.508 (± 0.545) log TP − 1.130 (r^2 = 0.20; n = 32).

The predictive powers of the MEI and MEI(C) were noticeably weaker (r^2 = 0.19 and 0.29, respectively) for PHYTO but were surprisingly better than TP in this regard (r^2 = 0.17; Table 6). Consistent with previous analyses, TN emerged as the best overall predictor of algal biomass (r^2 = 0.59). There were only two significant predictors of HERB, TP and TN, with TN accounting for a larger portion of the variability (r^2 = 0.45). Neither MEI nor MEI(C) was significantly correlated with HERB. That TN emerged as the best overall predictor of CHL, PHYTO, and HERB in this study merits further attention because TP is usually considered the most limiting nutrient of algal biomass in lakes (Schindler et al. 1978). To control for possible confounding effects of different sample size, I performed regression analyses again on reduced data sets (n = 71 for CHL–nutrients, n = 38 for PHYTO–nutrients, and n = 32 for HERB–nutrients).

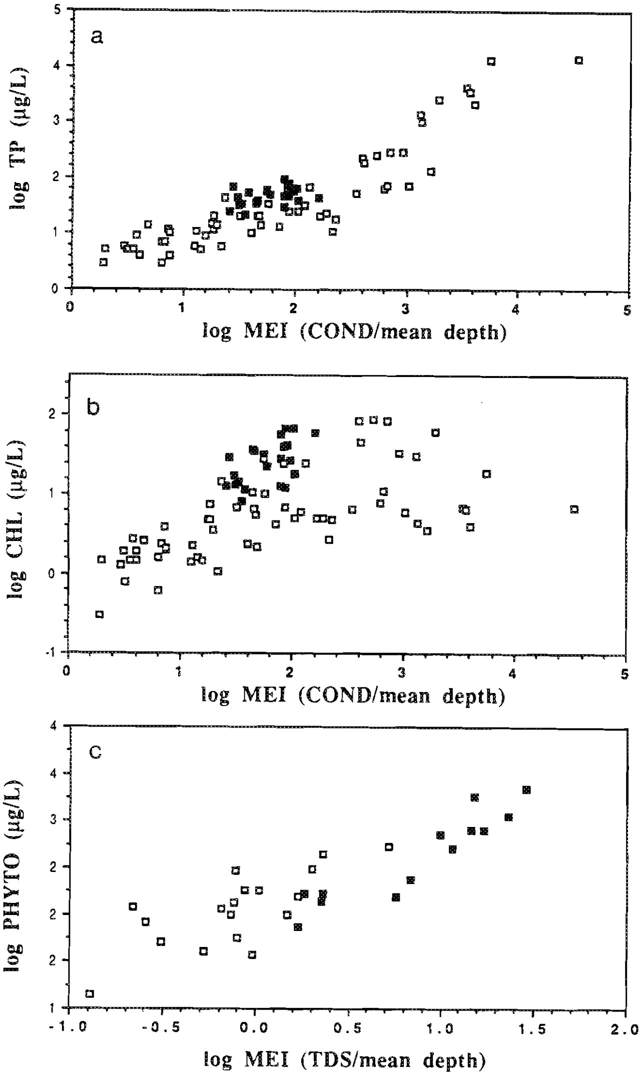

FIG. 10. (a) Log TP versus log MEI(C). Open circles are data from this study; closed circles are those from the independent data set (Jones and Hoyer 1982). (b) Log CHL versus log MEI(C). Symbols are the same as in Fig. 10a. (c) Log PHYTO versus log MEI. Open circles are data from this study; closed circles are those from the independent data set (Rawson 1960).

In the restricted data set, TP was considerably better than TN as predictor of CHL (r^2 = 0.87 versus 0.76, respectively; Fig. 9a). Thus, the superiority of TN noted in the earlier analyses probably reflected differences in sample size. By contrast, TN still emerged as the stronger predictor of PHYTO and HERB (r^2 = 0.62 versus 0.50 and 0.57 versus 0.20, respectively; Fig. 9b and 9c). Although this finding was unexpected, and the sample sizes in these latter cases were too small to allow conclusions to be drawn, more research should be conducted to determine the relative effectiveness of TP and TN for predicting standing stock at lower trophic levels when such factors as sampling time and analytical techniques can be standardized.

In this section, I have explored the relationship between MEI and nutrients and MEI and plankton biomass. Although conclusions are not possible because of limited data in some cases, it is clear that the MEI is a good predictor of TP and TN in lakes, capable of explaining 37–85% of the variation in nutrient concentrations. However, the predictive power of the index became progressively weakened with successive trophic levels (Table 6). It was marginally weaker than TN and TP for predicting CHL, but was ineffective for predicting HERB. Since the data set was extremely small, no conclusions regarding the possible uncoupling between the MEI and primary consumers can be made. Nevertheless, the source of the uncoupling between MEI and fish yield may stem from the inability of the MEI to accurately reflect zooplankton biomass, and further studies should be conducted to address this.

Test with Independent Data Set

I used data from the independent data set to evaluate the general applicability of empirical relationships developed here for other lakes. TP and CHL from Jones and Hoyer's (1982) study of shallow productive reservoirs were plotted against MEI(C) together with data from this study (Fig. 10a and 10b). There was generally good agreement between the literature and study data. The TP values in this study bracketed those of Jones and Hoyer, although their data appeared to cluster around the central portion of the range because they were all very shallow, well-mixed productive reservoirs with little variation in mean depth (ranging from 2.1 to 5.8 m). CHL values in this independent data set also overlapped with data in the upper portion of the range in this study, and in a few instances were higher than expected based on MEI(C). Unfortunately, I was not able to confirm the effect of mixing regime on the CHL–MEI relationship; when I regressed CHL against MEI and STRAT, stratification characteristic did not account for any significant amount of the variation in CHL.

I was able to use net plankton data from Rawson's (1960) study of large deep lakes to test the general effectiveness of the MEI for predicting PHYTO. Although there was little overlap in range between Rawson's data and those in this study, the respective trends were complementary (Fig. 10c). This suggests that the relationship between MEI and PHYTO established in this study can be applied to other lake types, and investigators should be encouraged to collect contemporaneous information on nutrients, plankton biomass, and fish yield for diverse lake types to rigorously test the generality of the MEI-biota relationships.

Summary

This study confirmed that important hydrologic (i.e. mixing regime and FR) and water transparency characteristics are significantly correlated with mean depth and that mean depth is better than A as an overall indicator of lake morphology. It also validated the basic assumption that TDS is a good surrogate of primary nutrients in lakes. Therefore, these assumptions of the MEI can be supported empirically. Despite this, the predictive power of the MEI became progressively weakened with increasing trophic level. While it accounted for up to 85% of the variation in TP and TN, it accounted for less than 50% of the variation in CHL, and none of the variation in HERB. This is problematic because the relationships between TP and various trophic levels are well documented (e.g. TP versus algal biomass (McQueen et al. 1986), TP vesus zooplankton biomass (Pace 1984), and TP versus fish biomass (Downing et al. 1990)). That MEI is a good predictor of nutrient concentrations, yet fails to accurately predict trophic levels above CHL in this study suggests that factors other than nutrients and lake morphometry regulate the standing stock of plankton in lakes (e.g. differences in hydrologic conditions). Future effort should be directed at increasing the sample size and standardizing analytical techniques and sampling times. This study also verified the significant effect of salinity on the MEI–CHL relationship and indicated that relationships should be constructed separately for saline and nonsaline lakes.

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