Relationships between Nannoplankton and Lake Trophic Status

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Relationships between Nannoplankton and Lake Trophic Status[1]

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The hypotheses that with increasing eutrophication (1) nannoplankton biomass increases and (2) the relative proportion (percent) of nannoplankton biomass decreases were tested with data from Lake Memphremagog, a lake exhibiting a nutrient gradient, and on a more general scale using published data from a number of lakes. Both hypotheses were supported within and among lakes if trophic status was defined by total algal biomass. This was also generally true if total phosphorus (TP) was used as an alternative measure of trophy, although percent nannoplankton biomass showed no relationship to TP among lakes. Empirical relationships that allow a first prediction of total nannoplankton biomass from total algal biomass or TP were calculated. The data suggest that among lakes, net plankton will show a more variable relationship with TP than nannoplankton.

Key words: nannoplankton, net plankton, trophic status, total biomass, total phosphorus

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Des données recueillies dans le lac Memphrémagog, un lac à gradient d'éléments nutritifs, ont servi à vérifier les hypothèses que (1) la biomasse de nannoplancton augmente et (2) la proportion relative (pour-cent) de la biomasse de nannoplancton diminue à mesure qu'augmente l'eutrophisation. On a également fait appel, dans un contexte plus général, à des données publiées sur plusieurs autres lacs. Les deux hypothèses sont confirmées, dans un même lac et d'un lac à l'autre, quand la biomasse algale totale est utilisée pour définir la condition trophique. Il en est généralement de même aussi quand le phosphore total (PT) est utilisé comme autre mesure de l'état trophique, bien que la proportion relative de la biomasse de nannoplancton ne montre pas de relation avec le PT entre lacs. Nous avons calculé les relations empiriques permettant une première prédiction de la biomasse totale de nannoplancton à partir de la biomasse algale totale ou du PT. D'après ces données, le plancton tamisé montrerait une relation plus variable avec le PT que le nannoplancton.

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TRADITIONALLY, algal communities have been investigated at the species level, which has resulted in the accumulation of a vast quantity of taxonomic data but which has led to few general predictions about patterns within and among lakes. An alternative, simpler method is to group phytoplankton assemblages into size fractions (e.g. Pavoni 1963; Semina 1972; Kalff 1972; Munawar and Munawar 1975). Although algal taxonomic divisions are not necessarily related to function, algal physiology and cell loss rates (through sedimentation and grazing) have been related to cell size (e.g. Laws 1975; Banse 1976; Smayda 1970; Burns 1968). The division of algal communities into size fractions may therefore allow the formulation of testable hypotheses about general relationships between environmental factors and phytoplankton size distributions.

In the past, most emphasis has been placed on the larger size fractions (or net plankton) because this group is primarily responsible for nuisance blooms; moreover, it is easier to identify and count. However, the importance of smaller size fractions has become recognized since it was shown that nannoplankton frequently make sizable contributions towards total algal production and biomass (e.g. Kalff 1972; Paerl and MacKenzie 1977; Munawar and Munawar 1975), and provide a major food source for herbivorous zooplankton (Burns 1968; Gliwicz 1967, 1977). In recognition of the functional roles of size fractions, Gelin and Ripl (1978) have redefined the nannoplankton as that size fraction which is ingestible by zooplankton grazers.

Whereas one of the major consequences of increased nutrient loading to lakes is a higher overall phytoplankton standing crop (e.g. Vollenweider 1969; Dillon and Rigler 1975; Nicholls and Dillon 1978), the existence of a general quantitative relationship between nutrient levels and nannoplankton standing crop has not been established. If, as evidence suggests, nutrient uptake rates are size dependent (e.g.

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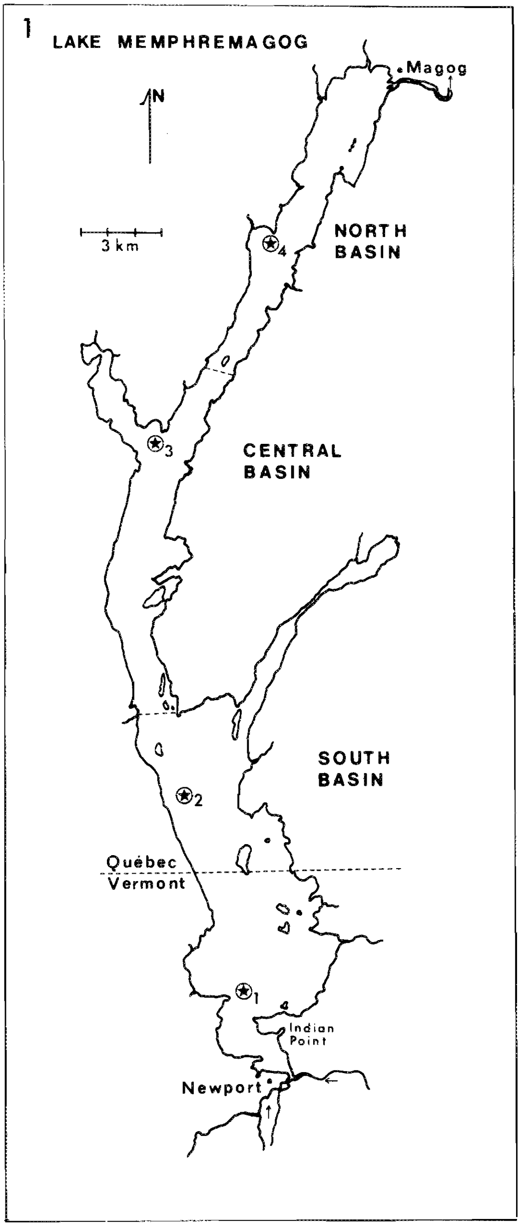

FIG. 1. Location of the four sampling stations in Lake Memphremagog.

Eppley et al. 1969; Laws 1975; R. Smith and J. Kalff, McGill University, Montreal, Que., unpublished data), and nutrient limitation plays a major role in size selection, then nannoplankton should exhibit some pattern in relation to nutrient concentration. In fact, evidence from previous investigations generally suggests a decrease in the relative proportion of nannoplankton with increasing eutrophication (Pavoni 1963; Semina 1972; Gelin and Ripl 1978; Spodniewska 1978, 1979).

The purpose of this study was to quantify the relationship between nannoplankton standing crop and lake trophic status, both within one lake exhibiting a nutrient gradient (Lake Memphremagog, Quebec – Vermont) and among a number of lakes covering a wide trophic range. Trophy is here defined by total algal standing crop (Vollenweider 1969), as measured by total algal biomass. Kalff and Knoechel (1978) and Nicholls and Dillon (1978) have shown that total biomass and total phosphorus (TP) are correlated, and because nannoplankton biomass is not independent of total biomass estimates, we reexamined the relationship between these two variables for our two data sets to use them as alternative measures of lake trophy, although there are problems associated with each (see Methods section). Using both of these measures within and among lakes, we then tested the hypotheses that (1) nannoplankton biomass increases but (2) the relative proportion (percent) of nannoplankton biomass decreases with increasing trophy.

Net plankton are generally more periodic in occurrence than nannoplankton (e.g. Munawar and Munawar 1975; Reynolds 1978), and therefore mean seasonal values of net plankton biomass should be more variable. We tested the prediction that net plankton biomass will exhibit more unexplained variance in relation to TP than nannoplankton biomass, and thus that any relationship between TP and total algal biomass is mainly a result of an underlying relationship between TP and nannoplankton.

Methods

Algal standing crop is usually represented by measurements of chlorophyll *a* (chl*a*) and biomass (estimated from cell volume assuming a density of 1.0 g/cm^3; Vollenweider 1969), and although neither measurement is entirely satisfactory, we chose to use total biomass. Cellular chl*a* content fluctuates over a wide range of physical and chemical conditions (0.1 – 9.7% fresh weight; Nicholls and Dillon 1978), and nannoplankton generally have a higher chl*a* content per unit cell volume (Paasche 1960; Manney 1972; Malone et al. 1979), which may inflate estimates of their relative contribution to total algal standing crop. Furthermore, measurements of nannoplankton chl*a* usually involve fractionation by screens, which do not give consistent results (Sheldon and Sutcliffe 1969; Malone et al. 1979). With algal biomass computed from cell volume, there is error associated with estimates of mean cell volume (e.g. Willén 1976), while the proportion of noncytoplasmic cell volume may be appreciable, especially for communities dominated by net plankton assemblages (Paasche 1960; Nalewajko 1966; Sicko-Goad et al. 1977). Although some authors have used correction factors for a few taxonomic groups (e.g. Smayda 1965; Devaux 1977), the proportion of noncytoplasmic cell volume has been shown to vary both between and within most taxonomic groups (Sicko-Goad et al. 1977). Nevertheless, a significant relationship has been found between uncorrected algal cell volume and dry weight (R. Peters, McGill University, Montreal, Que., unpublished data). We used total biomass (computed from uncorrected cell volume) as an estimate of plankton standing crop because the majority of published data on net plankton and nannoplankton are reported as such.

Mean summer TP concentration was used as an alternative to total biomass to measure lake trophy. Spring overturn values may give a better prediction of summer standing crop as measured by chlorophyll (e.g. Sakomoto 1966; Dillon and Rigler 1974) but mean summer values of TP and algal biomass are more strongly correlated than similar values of chl*a* and TP (Nicholls and Dillon 1978). Furthermore, Nicholls and Dillon (1978) found that spring TP was related quite closely to average summer concentrations.

LAKE MEMPHREMAGOG: NANNOPLANKTON AND TROPHIC STATE

The study lake is a 40-km-long glacial lake lying on the Quebec (Canada)–Vermont (USA) border (45°06′N, 72°17′W). It can be divided morphometrically into three major basins on the basis of mean depth (Fig. 1). The lake receives an estimated 84% of its phosphorus loading from three rivers entering the southern end of the lake at Newport, VT, resulting in a north–south nutrient gradient (Peters 1979), which is also reflected in variations in primary productivity and chl*a* (Ross and Kalff 1975).

Phytoplankton samples were collected every 1 or 2 wk from May to October (1976–77) at four stations located along the phosphorus gradient (Fig. 1). Average epilimnetic phytoplankton biomass was estimated from integrated tube samples, taken above the upper boundary of the thermocline or 15 m when there was no stratification. In the shallow southern basin, samples were taken down to 0.5 m above the sediments. Phytoplankton samples were fixed with Lugol's solution and later counted using the Utermöhl technique (Vollenweider 1969). Large species of low abundance were counted under low power across diagonal transects or over half the chamber area (minimum 26% total volume settled), whereas small or common species were counted under high power across one or two diagonal transects. Replicate counts showed a fairly low variance (with ±2 SE of 6 and 16% for total and nannoplankton biomass, respectively). The maximum particle size filtered by zooplankton appears to fall below 35–40 μm (Burns 1968), and we used an upper cell dimension of 35 μm to estimate nannoplankton biomass.

We obtained TP data for Lake Memphremagog from measurements made on samples taken from 2 m in depth at the three most southern stations in 1976 and at all four stations in 1977. The samples were analyzed for TP using a persulfate digestion technique (Johnson 1971).

To test the prediction that total algal biomass is significantly correlated with TP within Lake Memphremagog, we used least-squares regression analysis both with individually matched observations and mean seasonal values calculated for each station and year.

Using both total biomass and TP as trophic measures, we analyzed both individual and mean seasonal values by least-squares regression to test our two hypotheses. To assess the degree to which part–whole correlation accounts for any correlation between total and nannoplankton biomass (Sokal and Rohlf 1969), we also performed regression analysis between the two independent estimates of net plankton and nannoplankton biomass (the former obtained by difference), again using both individual and seasonal mean values. Finally, net plankton biomass (>35 μm; obtained by difference) and TP were used in least-squares regression to test the hypothesis that net plankton show a more variable relationship with TP than annoplankton.

AMONG LAKES: NANNOPLANKTON AND TROPHIC STATE

To test for generality of relationships between nannoplankton and lake trophy, we searched the literature for measures of total and nannoplankton biomass and TP. The data are summarized in Table 1. The total data set is available from the Depository of Unpublished Data, CISTI, National

TABLE. 1. Summary of the sources for data sets used for examining the relationships between nannoplankton and lake trophic status, as measured by total biomass (TB) and total phosphorus (TP).

			No. of data points with trophic measure as:	
Data source for biomass	Definition of nannoplankton (μm)	Data source for TP	TB (individual observations) (subset A)	TP (seasonal means) (subset B)
Granberg (1970)	60	Ilmavirta and Kotima (1974)	9	1
Kalff (1972)	64	Kalff (unpublished data)	5	1
Kristiansen (1971)	45	—	31	—
Munawar and Munawar (1975)	"Phyto-flagellates"	Weiler (1978); Dobson et al. (1974); Schelske et al. (1974); DiToro and Matystik (1979)	—	14
Pavoni (1963)	30 (some filaments)	—	7	—
Spodniewska (1978)	30	—	34	—
Spodniewska (1979)	30	Spodniewska (1979)	25	—
Spodniewska et al. (1973)	20	—	13	—
Watson (1979)	35	Watson (1979)	137	—
Watson (1979)	35	Watson (1979)	—	7
Watson (1979)	35	Watson (1979)	(52)[a]	(52)[a]

[a] Winthin-lakes test only.

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Most of the authors in the literature data set delineated the upper size limits of the nannoplankton fraction as 35 μm or less, although some used other criteria (Pavoni 1963; Munawar and Munawar 1975; see Table 1).

We took two subsets of the literature data to test the relationship between nannoplankton and the two measures of trophy, total biomass and TP.

Using total biomass as an estimate of trophic level, the widest trophic range was covered using individual observations: where only seasonal values of total and nannoplankton biomass were available (Table 1) these were not included in this subset (subset A). We obtained a total of 261 data points from seven different publications (Table 1). We also included individual observations from the four stations in Lake Memphremagog.

Using TP as a trophic measure (subset B), we obtained TP from the articles themselves or estimated it from other sources (Table 1). A total of 23 data points were obtained for this subset (Table 1); no individual observations were included. Only seasonal mean estimates of TP were available for most of the lakes in these data sets (except Lake Memphremagog), and thus we tested the relationship between TP and total algal biomass only for subset B, using least-squares regression analysis. We also used regression analysis with both subsets to test our two hypotheses (see introduction). For both subsets, we used analysis of covariance (type II, SAS 1980) to determine whether the different definitions of nannoplankton, different investigators, and differences in lake morphometry (as measured by surface area and mean depth where data were available) accounted for a significant amount of the total variance in nannoplankton biomass. To test the hypothesis that netplankton has a more variable relationship with TP than nannoplankton, we regressed netplankton biomass (obtained by difference) against mean seasonal TP for subset B.

Results

LAKE MEMPHREMAGOG: NANNOPLANKTON AND TROPHIC STATE

Data from within Lake Memphremagog supported hypotheses 1 and 2, using both total biomass and TP as measures of lake trophy. Both least-squares (model I) and functional (model II: Bartlett's three-group method, Sokal and Rohlf 1969) regression analysis gave statistically indistinguishable results for within- and among-lake tests, and only model I results are presented here. There was no relationship between individually matched observations of these two variables within Lake Memphremagog, but seasonal mean values for each station and year yielded a significant log – log correlation (Table 2, model I).

Using total biomass as a trophic measure, we found that nannoplankton biomass showed a highly significant logarithmic increase with total biomass (Table 2, model III). The slope of this relationship was significantly less than 1.0 ($P < 0.05$), and thus the relative proportion (percent) of nannoplankton biomass decreased significantly with increasing total biomass (Table 2, model IV). Nannoplankton biomass also showed a highly significant relationship with net plankton biomass ($P < 0.0001$; Table 2, model VII).

Using TP as a trophic measure, we obtained similar results.

TABLE. 2. Summary of regression models used to examine the relationship between nannoplankton and net plankton biomass (nanB and netB, respectively) and lake trophic status, as measured by total biomass (TB) and total phosphorus (TP). (*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$; ****$P < 0.001$.)

Test	n	b	(±2 SE)	a	r	p
Model I. log (TB) = $a + b$ log (TP)						
i) Within-lake test	7	2.02	(±0.58)	1.02	0.96	****
ii) Among-lakes test	23	1.43	(±0.35)	1.47	0.88	****
Model II. TB = $a + b$TP						
ii) Among-lakes test	23	161.09	(±39.14)	−593.42	0.87	****
Model III. log (nanB) = $a + b$ log (TB)						
i) Within-lake test	137	0.47	(±0.10)	1.20	0.62	****
ii) Among-lakes test	261	0.53	(±0.07)	1.03	0.70	****
Model IV. % nanB = $a + b$ log (TB)						
i) Within-lake test	137	−35.60	(±8.19)	151.12	0.60	****
ii) Among-lakes test	241	−25.36	(±4.48)	122.61	0.58	****
Model V. log (nanB) = $a + b$ log (TP)						
i) Within-lake test	7	0.83	(±0.56)	1.77	0.80	NS
ii) Among-lakes test	23	1.28	(±0.21)	1.24	0.93	****
Model VI. % nanB = $a + b$ log (TP)						
i) Within-lake test	7	−72.8	(±42.24)	111.97	0.84	NS
Model VII. log (nanB) = $a + b$ log (netB)						
i) Within-lake test	137	0.22	(±0.09)	2.06	0.39	****
ii) Among-lakes test	261	0.32	(±0.06)	1.82	0.53	****
Model VIII. log (netB) = $a + b$ log (TP)						
i) Within-lake test	7	2.52	(±0.75)	0.29	0.95	****
ii) Among-lakes test	23	1.67	(±0.52)	0.94	0.82	****

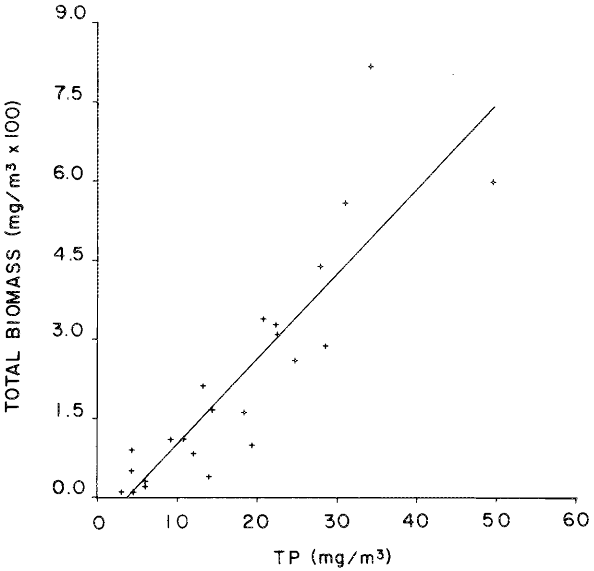

FIG. 2. Linear relationship between total biomass (TB) and total phosphorus (TP) among lakes, expressed by the equation:

$$TB = 161.09TP - 593.42.$$

As was shown above for total biomass, individual observations of both nannoplankton or net plankton biomass and TP showed no relationshp ($P > 0.05$), but seasonal mean values yielded significant positive correlations whereas there was a corresponding decrease in the relative proportion of nannoplankton biomass (Table 2, model VI). Seasonal mean net plankton biomass was more significantly correlated with mean TP than nannoplankton biomass (Table 2, models V and VIII).

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Data from among lakes also generally supported the hypotheses. Total biomass and TP were again highly correlated on a linear and log scale (Table 2; Fig. 2).

With total biomass as a measure of increasing trophy, nannoplankton again showed a highly significant logarithmic increase similar to that found within Lake Memphremagog (Table 2, model III; Fig. 3A):

$$(1) \quad \log(\text{nanB}) = 0.53 \log(\text{TB}) + 1.03.$$

The relative proportion (percent) of nannoplankton biomass showed a corresponding decrease (Table 2, model IV; Fig. 3B). Nannoplankton and net plankton biomass were again significantly correlated (Table 2, model VII).

Using TP as a measure of increasing trophic status, there was a highly significant logarithmic increase in nannoplankton biomass (Table 2, model V; Fig. 4):

$$(2) \quad \log(\text{nanB}) = 1.28 \log(\text{TP}) + 1.24.$$

However, there was no corresponding trend in percent nannoplankton biomass. Analysis of covariance showed that a small but statistically significant amount of the variance in nannoplankton biomass was attributable to differences between investigators and in nannoplankton size ranges used for individual observations (subset A) only (Table 3) whereas the variance accounted for by surface area and mean depth was not significant for either subset.

Net plankton biomass showed a highly significant logarithmic correlation with TP. A comparison of F values showed that TP accounted for more of the total variance in nannoplankton than net plankton biomass (Table 2).

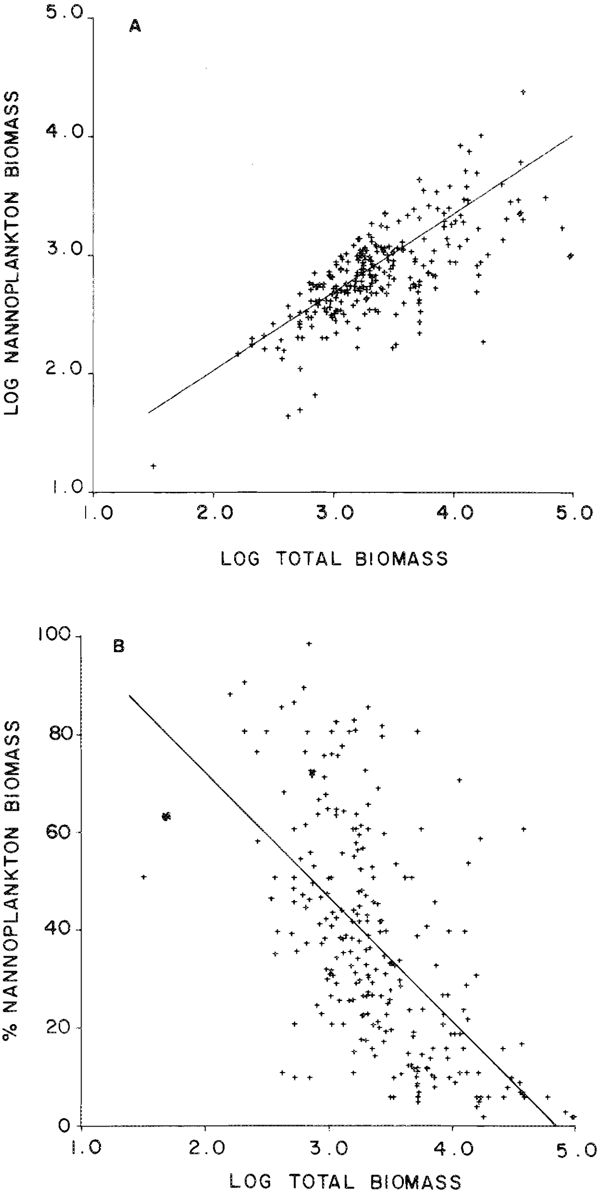

FIG. 3. General relationship between nannoplankton biomass (nanB) and total biomass (TB) among lakes, expressed by the equations:

$$(A) \quad \log(\text{nanB}) = 0.53 \log(\text{TB}) + 1.03.$$

$$(B) \quad \%\,\text{nanB} = -25.36 \log(\text{TB}) + 122.61.$$

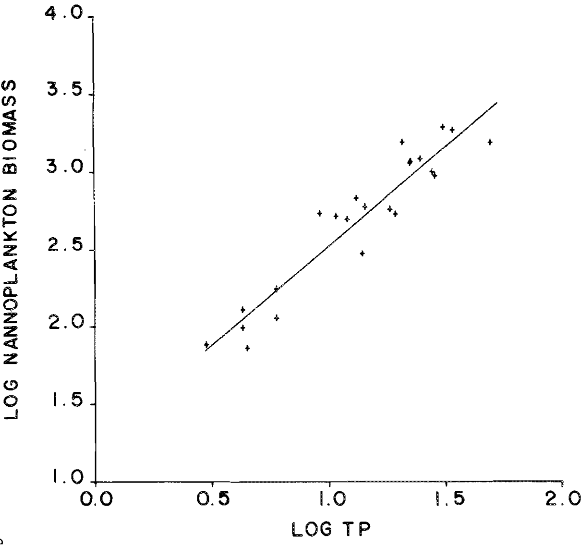

FIG. 4. General relationship between nannoplankton biomass (nanB) and total phosphorus (TP) among lakes, expressed by the equation:

$$\log(\text{nanB}) = 1.28 \log(\text{TP}) + 1.24.$$

Discussion

TP and total biomass were correlated only when seasonal means of these variables were used (Table 2, model I). Spodniewska (1979) also found no significant relationship for individual measurements of TP and total biomass for a number of Polish lakes. We therefore concluded that whereas mean seasonal TP provides an alternative to total biomass as a measure of the trophic status of lakes within our data sets, single measurements of TP do not necessarily reflect lake trophy. It is possible that the observed lack of correlation between individual measurements of total biomass and TP may be the result of a disequilibrium between phytoplankton biomass and the proportion of TP that is available (e.g. Peters 1979) and/or other size-selective factors affecting phytoplankton growth (e.g. Banse 1976) or losses through respiration, grazing, and sedimentation (Laws 1975; Banse 1976; Gliwicz 1967, 1977).

If total biomass is used as a measure of trophic state, the hypothesis that with increasing trophy there is (1) an increase in nannoplankton biomass and (2) a decrease in the relative proportion of nannoplankton biomass is supported by data within Lake Memphremagog and on a broader scale among lakes, despite the observed scatter (Table 2, model III; Fig. 3). The relationship between independent estimates of net plankton and nannoplankton biomass was highly significant both within and among lakes ($P < 0.0001$; Table 2, model VII), and we therefore concluded that the observed regressions between nannoplankton and total biomass (Table 2, model III) make valid predictions and are not simply a result of part–whole correlation. There is no question that the regressions between percent nannoplankton and total biomass involve part–whole correlation, but because the slopes of the regressions between nannoplankton and total or net plankton biomass are significantly less than 1.0, we still concluded that the relative proportion of nannoplankton biomass decreased with increasing trophy. This implies that at higher nutrient levels, either net plankton have higher growth rates or nannoplankton suffer greater losses, for example, through grazing.

There was no significant correlation between individual estimates of TP and nannoplankton biomass within Lake Memphremagog. However, we found that individual values of TP are also not a good measure of lake trophy, and the lack of correlation between these two variables does not contradict our hypotheses. Seasonal mean values of nannoplankton biomass and TP showed a significant positive correlation, both within Lake Memphremagog and among lakes (Table 2, model V), supporting the hypothesis that nannoplankton biomass increases with increasing trophy. However, the predicted corresponding decrease in the relative proportion (percent) of nannoplankton biomass was only observed within Lake Memphremagog, and was lacking among lakes. This suggests that among lakes covering a wide range of physical and chemical conditions, factors other than TP have more influence on the relative contribution of nannoplankton, whereas within the one lake we studied the factors are internally more constant and TP alone accounted for a highly significant amount of the total variance in mean seasonal percent nannoplankton biomass. Absolute nannoplankton biomass was strongly correlated with TP among lakes, and it appears that it is the net plankton which is more influenced by factors other than TP, or as we stated in our hypothesis, the net plankton have a less predictable relationship with TP than nannoplankton. A comparison of F values (Table 2: model V, $F = 8.96$ (i), 141.69 (ii); model VIII, $F = 45.56$ (i), 41.89 (ii)) shows that although this is not true within Lake Memphremagog, in general among lakes mean seasonal TP accounts for more variance in nannoplankton than in net plankton biomass. Analysis of covariance suggests that this is not an artifact of differences in technique between investigators (Table 3). Thus the general relationship between TP and total biomass (Fig. 2) is more attributable to the nannoplankton than the net plankton fraction. It is worth noting that although differences in lake morphometry did not account for a statistically significant amount of the total variance in net plankton biomass ($P < 0.053$, Table 3), mean depth accounted for more variance in net plankton than nannoplankton biomass, suggesting differential sedimentation losses.

The empirical relationships presented (equations (1), (2); Fig. 3, 4) allow a first prediction of nannoplankton biomass from total biomass or TP, which is useful for estimating trends in secondary production (McCauley and Kalff 1981). These models can eventually be refined to account for more of the unexplained variance, by incorporating other variables. Differences in technique between investigators, in the nannoplankton size ranges used, or in lake morphometry account for only a small amount of the total variance (Table 3), suggesting that the scatter around the regression lines (Fig. 3, 4) has a biological basis.

In summary, the hypotheses that with increasing trophy nannoplankton biomass increases while the relative proportion of nannoplankton decreases are generally supported by data within and between lakes. Furthermore, the empirical

TABLE. 3. Analyses of covariance (type II, SAS 1980) used to determine the relative effect of factors other than lake trophy (netB, TP) on nannoplankton and net plankton biomass (nanB, netB, respectively). Net plankton biomass is used instead of total biomass as a measure of trophy because it is independent of nannoplankton biomass. In the models presented here, the factors are nannoplankton size ranges used (size), author, and mean depth (z). (*$P < 0.05$; **$P < 0.01$; ***$P < 0.005$; ****$P < 0.001$.)

Model I. $\log(\text{nanB}) = a \log(\text{netB}) + b\text{size} + c \log(\text{netB}) * \text{size}$
Model II. $\log(\text{nanB}) = a \log(\text{netB}) + b\text{author} + c \log(\text{netB}) * \text{author}$
Model III. $\log(\text{nanB}) = a \log(\text{TP}) + bz + c \log(\text{TP}) * z$
Model IV. $\log(\text{netB}) = a \log(\text{TP}) + bz + c \log(\text{TP}) * z$

	Source of variance	P		Source of variance	P
	Subset A (n = 261)			Subset B (n = 23)	
I.	Full model	****	III.	Full model	****
	Log (netB)	****		Log (TP)	****
	Size	NS		z	NS
	Log (netB) *size	NS		Log (TP) *z	NS
	$R^2 = 0.395$			$R^2 = 0.973$	
II.	Full model	****	IV.	Full model	****
	Log (netB)	****		Log (TP)	****
	Author	****		z	NS
	Log (netB) *author	NS		Log (TP) *z	NS
	$R^2 = 0.417$			$R^2 = 0.977$	

models derived from these data allow the prediction of nannoplankton biomass from two alternative measures of trophic status, total algal biomass and total phosphorus.

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