

## The contribution of picophytoplankton in marine and freshwater systems of different trophic status and depth

**Abstract**—Although there are a number of single system and regional studies on the importance of picophytoplankton (PP; 0.2–2  $\mu\text{m}$ ), there has been little effort to quantify their importance on a larger scale and to integrate marine and freshwater studies. We developed empirical models from data in the literature to assess the absolute and relative importance of PP in marine and freshwater. The PP biomass (chlorophyll *a* [Chl *a*]) increases with trophic status, here represented by the total Chl *a*, in both marine and freshwater systems. In addition, PP abundance in freshwater, and primary production in marine waters, increases with trophic status. Even so, the relative importance of the PP biomass and primary production declines systematically with increasing trophic status in both marine and freshwater systems. Both the absolute biomass of PP and the relative contribution of PP biomass to the total phytoplankton community biomass are larger in freshwater at any particular value of total Chl *a*. In eutrophic lakes, which are typically shallow and particularly susceptible to the greatest phytoplankton resuspension and sediment recruitment, the on average small relative contribution of PP biomass appears affected by a relatively high but variable contribution of resuspended microplankton.

There has been considerable work on comparing the size structure of plankton communities in waters of different trophic (nutrient) status (e.g., Kalff 1972; Sprules and Munawar 1986; Watson and McCauley 1988; Chisholm 1992; Agawin et al. 2000). Studies have shown on average that the biomass of the small phytoplankton (the nanoplankton; 2–20  $\mu\text{m}$ ) increases with nutrient richness (trophic status) but that their biomass relative to larger plankton declines. The relative importance of small plankton therefore tends to decrease with increasing nutrient load. Two linked hypotheses have been put forward to explain this phenomenon. First, although the small phytoplankton do not appear competitively disadvantaged at high nutrient levels and suffer small sedimentation losses, their biomass increase is nevertheless constrained by high loss rates that are at least in part the result of predation. Second, the larger of the microalgae (approximately >70  $\mu\text{m}$ ) not only compete better for nutrients in nutrient-rich waters but in addition are little preyed upon, at least by freshwater macrozooplankton, commonly allowing them to dominate eutrophic waters (Watson and McCauley 1988). Although an appreciable number of the microplankton are not subject to sedimentation as the result of motility or of buoyancy control, sedimentation rates tend to be higher for larger algae (e.g., Riegman et al. 1993; Raven 1998). System depth is therefore a factor that might confound the relationship between the contribution of different size fractions and trophic status.

The discovery of small (0.2–2.0  $\mu\text{m}$ ) picophytoplankton (PP) during the late 1970s led to considerable research examining whether the previous models of average size as a

function of trophic status remained valid (Stockner 1991). Several regional studies have shown, as had been quantified earlier for the nanoplankton (Watson and Kalff 1981), that the relative importance of PP declines with increasing trophic status. The importance of PP has received several reviews based on limited data (Fogg 1986, 1995; Stockner and Antia 1986; Stockner 1988; Stockner and Shortreed 1991), but until very recently (Agawin et al. 2000) without the development of broadly based quantitative models and as yet without attempts to contrast and compare data from marine and freshwater environments.

Our aim is to develop such models to assess and predict the relative and absolute importance of PP abundance, biomass, and production in aquatic systems of different trophic status from data in the literature. Our second goal is to test the hypothesis that the PP response to environmental factors does not differ systematically between marine and freshwaters. Although our comparative data cannot distinguish between the two mechanisms (above) that might drive patterns of phytoplankton size, we explore a third possible hypothesis: that the importance of the PP is determined in part by the sedimentation and resuspension or emergence of the microplankton.

**Methods**—We performed literature searches for articles that contained data on total phytoplankton biomass and picophytoplankton biomass, production, or abundance. Picophytoplankton were defined as phytoplankton <3  $\mu\text{m}$ , but we included data from studies where only the biomass of phytoplankton <2 or <1  $\mu\text{m}$  were reported. Restricting the data to phytoplankton <2  $\mu\text{m}$  does not qualitatively alter the outcome of our analyses. We used chlorophyll *a* (Chl *a*) concentration as the measure of biomass, both because the data were so reported and because it separates the photo-trophic from the heterotrophic plankton. Trophic status was estimated from the phytoplankton community biomass (total Chl *a*). Mean depth in lakes was also taken from the literature and used as an additional independent variable that might be expected to influence PP abundance, biomass, and production.

Data were extracted from 91 studies, of which 22 were freshwater and 69 were marine. Freshwater data were almost exclusively from temperate zone, dimictic lakes. Marine studies encompassed all of the world's oceans and included data from tropical, subtropical, temperate, and polar regions, as well as some inland seas, especially the Mediterranean and Arabian, and both coastal and offshore environments. Estuarine data were excluded from the analysis because there were too few to conduct comparisons with the other systems. Freshwater data points are nearly all from summer sampling, whereas many of the marine data points are from samples taken year-round. Multiple data points from a single lake or

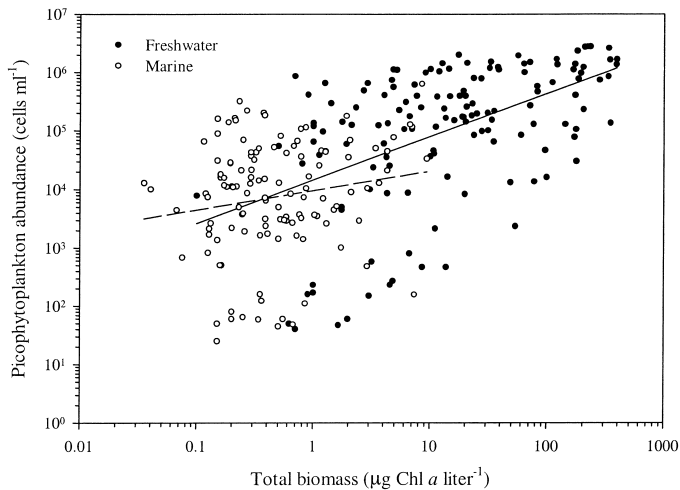


Fig. 1. Relationship between picophytoplankton abundance (cells  $\text{ml}^{-1}$ ) and total phytoplankton biomass ( $\mu\text{g Chl } a \text{ L}^{-1}$ ). The solid line is the regression line for freshwater data, and the dashed line is for marine data.

marine station were averaged among studies or sampling dates to avoid autocorrelation among data points. Depth integrated Chl *a* and production estimates (e.g.,  $\text{mg Chl } a \text{ m}^{-2}$ ) were divided by the integration depth to obtain average values per volume of water. A list of the studies used for this analysis is available from the authors upon request.

Least-squares (Model I) linear regression analysis was used because we were primarily interested in prediction. Geometric-mean regressions (Model II, Sokal and Rohlf 1995) were also computed to allow for the possibility that the regression coefficients (slopes) could be sufficiently underestimated to change interpretations due to errors in the independent variable. It is apparent that the community biomass includes the PP biomass and that there is, therefore, an unavoidable covariation that is most pronounced in highly oligotrophic waters. We hope that the empirical patterns described will stimulate the collection of the much-needed additional data both to expand the all-too limited database and to evaluate our necessarily speculative interpretations.

Table 1. Summary of the relationships between measures of absolute and relative (%) picophytoplankton (PP) abundance (abund; cells  $\text{ml}^{-1}$ ), biomass (Chl *a*;  $\mu\text{g L}^{-1}$ ), and primary production (prod;  $\mu\text{gC L}^{-1} \text{ d}^{-1}$ ), and measures of total algal biomass (Tchl *a*;  $\mu\text{g L}^{-1}$ ) for marine (M) and freshwater (F). *SE* and *F* are the standard error and *F*-statistic of the model. *GM slope* is the slope of the geometric mean regression model, and *Overlap?* indicates whether the 95% confidence intervals of the GM slope do (Y) or do not (N) overlap with those of the least-squares regression slope.

Figure	F or M	Model	$r^2$	<i>n</i>	SE	<i>F</i>	<i>p</i>	GM slope	Overlap?
1	F	$\log_{10}(\text{PPabund}) = 4.16 + 0.74 \log_{10}(\text{TChl } a)$	0.25	137	1.02	44.1	<0.0001	0.30	Y
	M	$\log_{10}(\text{PPabund}) = 3.98 + 0.33 \log_{10}(\text{TChl } a)$	0.03	122	0.960	3.5	0.051	7.20	N
	F+M	$\log_{10}(\text{PPabund}) = 4.13 + 0.73 \log_{10}(\text{TChl } a)$	0.34	259	1.01	131.4	<0.0001	4.43	N
2	F	$\log_{10}(\text{PPChl } a) = -0.43 + 0.47 \log_{10}(\text{TChl } a)$	0.31	178	0.541	77.7	<0.0001	0.50	Y
	M	$\log_{10}(\text{PPChl } a) = -0.60 + 0.46 \log_{10}(\text{TChl } a)$	0.27	524	0.341	194.1	<0.0001	1.59	N
3	M	$\log_{10}(\text{PPprod}) = 0.86 + 0.39 \log_{10}(\text{TChl } a)$	0.10	165	0.450	14.1	0.0002	1.83	N
4	F	$\log_{10}(\% \text{PPChl } a) = 1.56 - 0.53 \log_{10}(\text{TChl } a)$	0.36	178	0.542	99.6	<0.0001	0.91	Y
	M	$\log_{10}(\% \text{PPChl } a) = 1.40 - 0.54 \log_{10}(\text{TChl } a)$	0.34	524	0.340	274.3	<0.0001	3.08	N
5	F	$\% \text{PPprod} = 30.26 - 16.98 \log_{10}(\text{TChl } a)$	0.41	40	14.84	26.1	<0.0001	35.53	Y
	M	$\% \text{PPprod} = 43.36 - 23.39 \log_{10}(\text{TChl } a)$	0.13	168	21.03	24.95	<0.0001	61.51	Y

*Absolute importance of picophytoplankton*—There is a significant positive relationship between PP abundance and total Chl *a*, a measure of trophic status, in freshwater (Fig. 1, Table 1), although there is considerable variation in the relationship. This particular relationship has been previously quantified regionally (Burns and Stockner 1991; Stockner and Shortreed 1991) but has not been evaluated for such a large number of lakes or over such a large biomass range. Although there is no relationship between PP abundance and total Chl *a* in marine waters (Table 1), the regression model including both marine and freshwater data is a considerably better fit than when marine data are used alone (Table 1), which suggests that there might be insufficient variation in total Chl *a* values for the marine data to adequately predict the PP abundance. The regression model including both marine water and freshwater data is statistically indistinguishable from the freshwater regression model.

As previously demonstrated for the freshwater nanoplankton (Watson and McCauley 1988), the PP biomass increases with increasing community biomass in both marine waters and freshwaters (Fig. 2, Table 1). Although the slopes of the regression lines for marine water and freshwater data do not differ ( $p > 0.1$ ), the intercepts differ significantly ( $t = 5.8$ ,  $p < 0.0005$ ), indicating a consistently larger PP biomass at any particular community biomass in freshwater. Calculations using the regression models (Table 1) indicate that PP biomass in freshwater is 1.5 times higher than in marine environments at a community biomass of  $1 \mu\text{g Chl } a \text{ L}^{-1}$  and rises to 3.4 times greater at the upper limit of community biomass ( $18.2 \mu\text{g Chl } a \text{ L}^{-1}$ ) for the marine systems used in our analysis.

The much more limited production data (Fig. 3) show that PP community production rates in marine waters increase with trophic status, although the fraction of the variation explained is minimal. Equivalent freshwater data are virtually lacking. A significant and positive relationship between total algal biomass and PP production was reported previously in a regional study of shallow Florida lakes for phytoplankton  $<5 \mu\text{m}$  (Carrick and Schelske 1997), but such a relationship was not observed in the Baltic Sea (Larsson and Hagström 1982). Given the great paucity of PP production

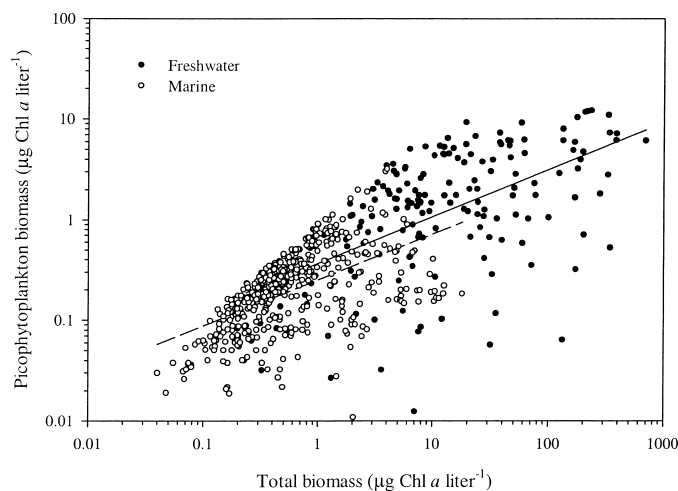


Fig. 2. Relationship between picophytoplankton biomass and total phytoplankton biomass (both in  $\mu\text{g Chl } a \text{ L}^{-1}$ ). The solid line is the regression line for freshwater data, and the dashed line is for marine data.

studies, above all in freshwater, there is a great need for more data. Future studies should use a standardized and well-quantified technique for separating the PP because the different filter types in use add considerably to the observed variability in both PP biomass and production rates within and among systems studies (see Stockner and Antia 1986; Carrick and Schelske 1997).

**Relative contribution of picophytoplankton**—Several regional freshwater studies in Denmark, Japan, Poland, and Canada (see Stockner and Shortreed 1991; Takamura and Nojiri 1994; Søndergaard 1997; Szlag-Wasielewska 1997) have reported a decline in the relative contribution of PP to the community biomass with increasing trophic status but, with one exception (Szlag-Wasielewska 1997), did not quantify the relationship. The present results (Fig. 4) confirm earlier speculation (e.g., Stockner 1991) about the expected decline in the relative importance of the PP in more eutrophic, high algal biomass freshwater systems (Fig. 4, Table 1) and support the recently reported conclusions drawn globally for marine systems (Agawin et al. 2000). Although there is no significant difference between the marine and freshwater slopes (Fig. 4,  $p > 0.1$ ) the intercepts once again differ ( $t = 6.8$ ,  $p < 0.0005$ ) with the PP biomass 1.5 times greater in freshwater at a community biomass of  $1 \mu\text{g Chl } a \text{ L}^{-1}$ . Freshwater PP typically contributes more than 50% of the total biomass in ultraoligotrophic waters at a community biomass of approximately  $0.54 \mu\text{g Chl } a \text{ L}^{-1}$  ( $< 1 \mu\text{g TP L}^{-1}$ ), declining in hypertrophic waters to, on average, 3% at concentrations of  $100 \mu\text{g Chl } a \text{ L}^{-1}$ . The marine PP dominates ( $> 50\%$ ) the community biomass at  $0.28 \mu\text{g Chl } a \text{ L}^{-1}$  and is predicted to decline to the same average of 3% when the community biomass rises to only  $51.2 \mu\text{g Chl } a \text{ L}^{-1}$  rather than the  $100 \mu\text{g Chl } a \text{ L}^{-1}$  predicted in freshwater (Fig. 4). The decline in the contribution of the PP to the community biomass in more eutrophic systems is not restricted to the largest among the PP because Chisholm (1992) reported a similar decline in the contributions of the smallest ( $< 1 \mu\text{m}$ )

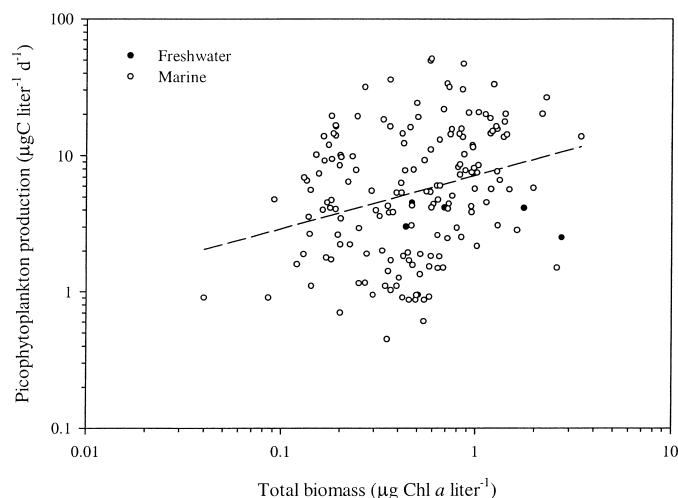


Fig. 3. Relationship between picophytoplankton production ( $\mu\text{gC L}^{-1} \text{ d}^{-1}$ ) and total phytoplankton biomass ( $\mu\text{g Chl } a \text{ L}^{-1}$ ). The dashed line is for the marine data only.

fraction in marine waters. The observed relative decline in the contribution of the PP biomass to the community phytoplankton biomass in more productive waters is accompanied by an equivalent relative decline in their contribution to the community primary production with increasing trophic status in freshwater and marine systems (Fig. 5, Table 1), although there are relatively few freshwater data.

**Discussion**—The abundance in freshwater (Fig. 1), biomass in freshwater and marine waters (Fig. 2), and production in marine systems (Fig. 3) of the PP increase, on average, with trophic status (total Chl *a*). Consequently, eutrophic systems contain more PP than their more oligotrophic marine and freshwater counterparts. The results of a recent review (Agawin et al. 2000) are qualitatively similar

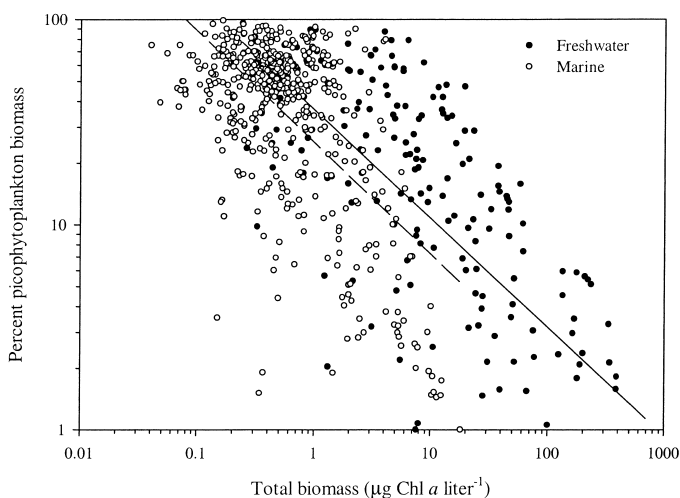


Fig. 4. Relationship between the percent contribution of picophytoplankton biomass to total phytoplankton biomass and total phytoplankton biomass ( $\mu\text{g Chl } a \text{ L}^{-1}$ ). The solid regression line is for freshwater data, and the dashed line is for marine data.

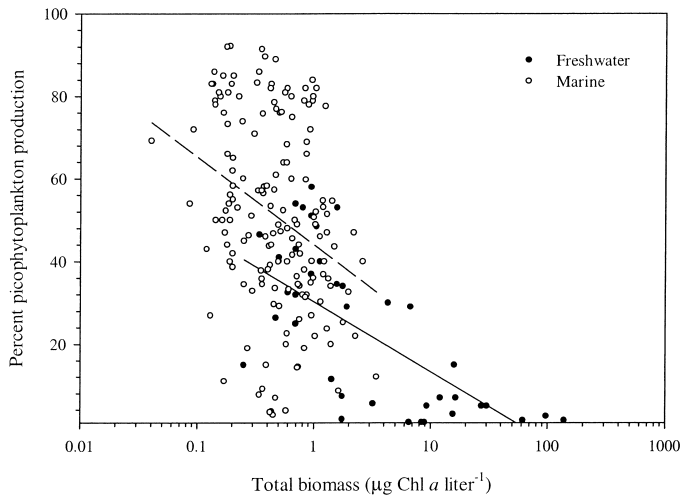


Fig. 5. Relationship between the percent contribution of marine picophytoplankton to total primary production and total phytoplankton biomass ( $\mu\text{g Chl } a \text{ L}^{-1}$ ). The solid regression line is for the freshwater data, and the dashed line is for the marine data.

to those obtained for marine waters in Figs. 2 and 4 of the present study. A statistical comparison of the regression slopes would be inappropriate because many of the data points in the two studies overlap. Geometric-mean regressions were calculated (Table 1) and were in qualitative agreement with the model I regressions. However, the overlap of the 95% confidence intervals in only five of the 10 regression models indicates that some of the variation in the models is explained by error in the measurement of the community biomass.

The abundant marine data indicate that PP production (Fig. 3) increases more slowly with increases in trophic status than does the PP biomass (Fig. 2). The data cannot resolve whether the progressively slower increase in PP production reflects a decreasing PP loss rate in more productive waters or is an artifact of the methods used for separating the phytoplankton size fractions. An increased plugging in more eutrophic waters of the filters used to separate the PP from the nanoplankton and microplankton would also produce a progressively increasing underestimation of the PP production in more eutrophic waters (Furnas 1987).

Even though the absolute abundance and biomass of PP both rise with trophic status, their relative contribution declines systematically in both marine water and freshwater. The relative PP decline in more eutrophic waters is qualitatively similar to conclusions drawn previously for the freshwater nanoplankton (Watson and McCauley 1988).

Although the community biomass (Chl *a*) is a useful in-

dicator of the relative and absolute contribution of the PP to the biomass, there is much unexplained variation, some of which is probably attributable to variable predation and other losses suffered by the PP and to temporal and spatial variation in sedimentation and resuspension of microplankton. Even so, it is evident that the absolute and relative contribution of the PP to the algal biomass is consistently higher in freshwater (Table 1). It is certainly possible that the on average 1.5-fold higher PP biomass in freshwater at a community biomass of  $1 \mu\text{g Chl } a \text{ L}^{-1}$  reflects a systematically higher absolute PP loss rate in the sea (due, for example, to predation or lysis) than in freshwater (Fig. 2). However, the relative contribution of PP to the total community biomass is also smaller in the marine systems (Fig. 4). We hypothesize that the discrepancy reflects primarily associated differences in system morphometry. Lakes are typically shallow compared to even the coastal seas. Furthermore, lakes tend to be small and have a typically lower fetch resulting in a much thinner mixed layer in those systems deep enough to stratify. Therefore lake epilimnia allow a much greater loss of sedimenting microplankton from the mixed layer during a few calm days than would be the case for their typically much thicker marine counterparts, which yields the observed higher proportion of PP in lakes.

Unfortunately, depth and trophic status for the freshwater data are highly correlated (Table 2), with the more eutrophic lakes typically also shallow, whereas oligotrophic lakes tend to be much deeper. Multiple regression models using both depth and trophic status therefore perform no better than each does singly. However, simple regression models show that depth in freshwater is an equally good indicator of PP biomass and its contribution to the community biomass as trophic status (Table 2).

Although the correlation between trophic status and depth confounds a causal interpretation, such an interpretation is suggested by research on a shallow (mean  $z = 1.7 \text{ m}$ ) hypertrophic Florida lake (Carrick et al. 1993; Schelske et al. 1995; Carrick and Schelske 1997) and on 11 shallow ( $z_{\text{max}} = 2$  to  $3 \text{ m}$ ) oligotrophic Antarctic ponds (Andreoli et al. 1992). Both studies reveal an exceptionally large within or among system variation in the contributions of the PP to the total phytoplankton production or biomass.

Shallow waters in particular are highly susceptible to a periodic wind-induced resuspension of sedimented planktonic and littoral zone algae characterized by a benthic phase (meroplankton), which, when mixed into the overlying water, can double Chl *a* concentration in the water column of Lake Apopka, Florida, with the increase being overwhelmingly composed of previously sedimented microplankton (Carrick et al. 1993). Consequently, there is a good corre-

Table 2. Relationships between depth (m) and picophytoplankton (PP) abundance, biomass, and PP percent contribution to total biomass in lakes. Variables and units are as in Table 1.

Model	$r^2$	$n$	SE	$F$	$p$
$\log_{10}(\text{Tchl } a) = 1.54 - 0.69 \log_{10}(\text{depth})$	0.40	43	0.500	26.9	<0.0001
$\log_{10}(\text{PPabund}) = 3.00 - 1.02 \log_{10}(\text{depth})$	0.24	49	1.162	15.2	0.0003
$\log_{10}(\text{PPChl } a) = 0.87 - 0.73 \log_{10}(\text{depth})$	0.27	26	0.824	8.8	0.007
$\% \text{PPChl } a = 5.46 + 21.3 \log_{10}(\text{depth})$	0.32	20	18.50	8.6	0.009

lation between wind speed and algal biomass (Chl *a*) in the lake. Similarly, in the shallow western basin of Lake Erie the abundance of the diatom *Fragilaria crotonensis* increased sixfold 2 d after the resuspension of sediments following a storm (Hartig 1987). However, such findings are not restricted to lakes because Malone et al. (1983) noted a large contribution of wind resuspended microplankton (diatoms) to the phytoplankton biomass and its variability in a marine coastal zone.

The relative importance of picophytoplankton and nanophytoplankton could be expected to be greatest following the sedimentation of the denser microplankton during periods of low turbulence. This was demonstrated to be the case in shallow Lake Apopka, where the picophytoplankton and nanophytoplankton contributed about 35 and 54%, respectively, of the community biomass during periods of low turbulence and associated high microplankton (primarily diatom) sedimentation (Schelske et al. 1995). The contribution of the picophytoplankton (there  $<5 \mu\text{m}$ ) was more than tenfold greater than the about 2% predicted on the basis of trophic status alone (Fig. 4). Similarly, large phytoplankton often dominate the phytoplankton community in temperate coastal areas during the winter and spring but decline in importance during the summer stratification when they are more prone to sedimentation from the euphotic zone (e.g., Tamigneaux et al. 1999). We hypothesize that the role of system mean depth in predicting the relative and absolute importance of PP in the biomass (Table 2) represents, at least in part, the progressively smaller importance of resuspension in deeper temperate freshwater systems, characterized by a summer stratification and relatively steep underwater slopes, which expose a progressively smaller fraction of the sediments to wind-induced turbulence. Since lake size and depth are positively correlated in among lake studies (Duarte and Kalff 1989), the importance of the littoral zone as a source of algae to the open water will decline with increasing mean depth. We suspect, for equivalent reasons, that the 1.5-fold lower fraction of PP biomass in marine than in freshwater systems of the same trophic status primarily reflects differences in system morphometry (depth), with the, on average, much thicker marine mixed layer less subject to microplankton sedimentation losses during a series of calm days or to resuspension into their typically much thicker water columns. The hypothesis may explain the consistently higher variation (regression standard errors) in the freshwater regression models than in their marine counterparts (Table 1).

Although the meroplankton community biomass is dominated by large cells or colonies often highly subject to sedimentation from shallow water columns during periods of low turbulence, the PP too are a component of the meroplankton and can be abundant on sediments and on littoral zone vegetation (Thompson et al. 1997). But because the PP typically makes up an only minor fraction of the biomass in mesotrophic and eutrophic lakes (Fig. 4), their recruitment to the water column during windy periods is typically masked by a disproportionately large microplankton community biomass.

Whether the meroplanktonic component of the phytoplankton is recruited primarily from pelagic sediments, as in shallow wind exposed Florida lakes, or contributed by lit-

toral zone, benthic algae must depend on system morphometry (size, depth). Work on the large and deep (mean  $z = 100 \text{ m}$ ) Lake Constance (Austria, Germany, Switzerland) reported that approximately half of the 190 microplankton and nanoplankton species identified in the open water were primarily phyto-benthic species from the littoral zone. These meroplanktonic species contributed about a third of the open water community biomass (Schweizer 1997). But meroplankton are also important in small, less windswept lakes. Recently, Hansson (1996) noted that about one-third of the species in four small basins in the United States were in part recruited from the sediments, primarily from depths  $<4 \text{ m}$ . Their recruitment typically increased the phytoplankton abundance in the epilimnia by 10–50%  $\text{d}^{-1}$ .

In conclusion, the present study demonstrates predictable and generally similar patterns in the absolute and relative importance of PP in both freshwater and marine systems, with our conclusions regarding the sea confirmed by Agawin et al. (2000). The absolute biomass and the relative contribution is larger in freshwater at any particular value of total Chl *a*. We present preliminary evidence that the importance of PP is not only a function of trophic status but also linked to water column depth in freshwater. An evaluation of the literature indicates that depth plays a complementary role to trophic status in determining the size distribution of phytoplankton communities. It does so by affecting the resuspension and recruitment of meroplankton from sediments and the littoral zone vegetation, as well as by affecting the microplankton loss rates through sedimentation from the mixed layer.

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