Environmental control of diatom community size structure varies across aquatic ecosystems

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Changes in the size structure of photoautotrophs influence food web structure and the biogeochemical cycling of carbon. Decreases in the median size of diatoms within communities, in concert with climate warming and water column stratification, have been observed over the Cenozoic in the ocean and over the last 50 years in Lake Tahoe. Decreases in the proportion of larger plankton are frequently observed in response to reduced concentrations of limiting nutrients in marine systems and large stratified lakes. By contrast, we show a decrease in the median size of planktonic diatoms in response to higher nutrient concentrations in a set of intermediate-sized alkaline lakes. Climate-induced increases in the frequency, duration and strength of water column stratification may select smaller planktonic species in the ocean and larger lakes owing to a reduction in nutrient availability and sinking rates, while light limitation, stimulated by nutrient eutrophication and high chlorophyll concentrations, may select smaller species within a community owing to their high light absorption efficiencies and lower sinking rates. The relative importance of different physiological and ecological rates and processes on the size structure of communities varies in different aquatic systems owing to varying combinations of abiotic and biotic constraints.

Keywords: cell size; climate change; environmental change; eutrophication; macroecology; phytoplankton and diatoms

1. INTRODUCTION

Anthropogenic activities have resulted in large perturbations in nitrogen and phosphorus cycles (Schlesinger 1997). The addition of the macronutrients nitrogen and phosphorus to aquatic ecosystems leads to fundamental changes in ecosystem structure and function, including the following: increases in algal and plant biomass; reduced water clarity; taste and odour problems; decreases in deep-water dissolved oxygen concentrations; and changes in species abundance and diversity (Smith *et al.* 1999). Phytoplankton community structure responds rapidly to changes in limiting nutrient concentrations (Hall & Smol 1999). The strong relationship between the taxonomic structure of diatom assemblages with environmental conditions in lakes has led to the development of transfer functions that quantitatively estimate current and past environmental conditions, including total nitrogen and phosphorus concentrations, from the relative abundance of diatom species preserved in sediments (e.g. Hall & Smol 1999; Stoermer & Smol 1999; Reavie & Smol 2001; Reid 2005; Weckström 2006).

Field observations indicate that the size structure of phytoplankton communities is often affected by environmental concentrations. In marine systems, the most predominant pattern is an increase in larger phytoplankton cells as a proportion of total biomass and numerical abundance, with increasing total chlorophyll *a* concentration (Chisholm 1992; Li 2002) in response to the macronutrient nitrate (Tremblay *et al.* 1997; Duarte *et al.* 2000; Vidal & Duarte 2000) or the micronutrient iron (Tsuda *et al.* 2003). Observed changes in the size structure of the plankton, and specifically planktonic, periphytic and benthic diatom communities, in response to trophic status in freshwater systems, are more variable (Sprules & Munawar 1986; Cattaneo *et al.* 1998; Lavoie *et al.* 2006; Passy 2007). For example, phytoplankton communities within Lake Memphremagog in Quebec exhibit an increase in the relative abundance of larger cells under high nutrient concentrations (Watson & Kalff 1981; Peters 1983; Sprules & Munawar 1986). Similarly, analysis of periphyton from Lake Memphremagog and nine additional lakes from Quebec also showed an increase in algal cell volume with total phosphorus (TP) in the lakes (Cattaneo 1987). By contrast, the mean size of periphytic diatoms in streams and creeks along the St Lawrence River basin exhibits no significant relationship with TP concentrations (Lavoie *et al.* 2006).

There are several factors identified that could be responsible for the relationship between nutrient concentration and diatom community size structure, including the size dependence of nutrient and light acquisition

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and requirements for growth (Finkel *et al.* 2004, 2005; Irwin *et al.* 2006), and size-dependent sinking (i.e. Stoke's Law) regulated by changes in stratification (Rodríguez *et al.* 2001; Winder *et al.* 2009). Larger phytoplankton species generally have lower rates of intrinsic growth (Banse 1976; Schlesinger *et al.* 1981), photosynthesis (Taguchi 1976; Finkel 2001), respiration (Laws 1975), mass-normalized nutrient uptake (Eppley *et al.* 1969; Aksnes & Egge 1991) and lower nutrient requirements for positive growth (Shuter 1978; Grover 1989), as well as lower pigment-specific light absorption efficiencies (Morel & Bricaud 1981; Agustí 1991; Finkel *et al.* 2004). As a consequence, physiological models tend to predict that small cells will dominate under low nutrient conditions, and the relative proportion of smaller cells in an assemblage will increase with decreasing nutrient concentration (Irwin *et al.* 2006). Predation, viral attack and parasitic attack can also be size-dependent and interact with organism physiology to influence phytoplankton community size structure (Brooks & Dodson 1965; Thingstad 1998; Cyr & Curtis 1999; Armstrong 2003; Raven & Waite 2004; Raven *et al.* 2006). For example, it is hypothesized that ephemeral nutrient inputs cause a relative increase in the abundance of larger phytoplankton cells not only because the higher nutrient concentrations stimulate their growth but because their predators lag in their response to periodic nutrient inputs while the small cells are kept in check by their smaller microzooplankton grazers (Thingstad 1998; Armstrong 2003). Stratification and nutrient availability in many aquatic systems are strongly coupled, making it difficult to separate the relative importance of nutrient concentration relative to stratification and the size-dependent sinking rate in shaping the size structure of plankton communities (Rodríguez *et al.* 2001; Winder *et al.* 2009). Smol *et al.* (1984) hypothesized that the size of planktonic diatoms in lake assemblages decreases in response to increasing nutrient availability and associated increases in total chlorophyll *a* concentration in order to decrease sinking rate out of the euphotic zone, and Huisman & Sommeijer (2002) showed that sinking rate in natural systems is negatively correlated with water column turbidity, consistent with the model predictions that irradiance and turbulence can regulate the size structure of phytoplankton communities through their effects on growth and sinking rates.

A decrease in the size of phytoplankton will alter food web structure and the cycling of carbon (D'Hondt *et al.* 1998; Laws *et al.* 2000; Finkel 2007; Finkel *et al.* 2007). In marine ecosystems, large phytoplankton cells tend to be grazed by large zooplankton, resulting in shorter, simpler food webs that may result in more efficient matter and energy transfer (Ryther 1969). The larger and denser cells are responsible for the majority of organic carbon exported to the deep sea (Laws *et al.* 2000). Changes to climate are associated with shifts in water column stratification and the availability of light and nutrients in the surface ocean and stratified lakes, altering the types of niches available to planktonic and other organisms (Rutherford *et al.* 1999; Irwin *et al.* 2006). Macroevolutionary changes in the size of marine phytoplankton have been observed in response to changes in climate and water column stratification over the last 65 million years of Earth's history (Finkel *et al.* 2007). Analogously, a decrease in the median size of

diatoms in Lake Tahoe has been observed in response to climate-induced increases in water column stratification (Winder *et al.* 2009), and a shift towards smaller dominant planktonic diatom species (*Cyclotella*) has been observed across many high-latitude (Smol *et al.* 2005) and temperate (Rühland *et al.* 2008) North American and European lakes over the period of recent warming, manifested by decreased ice cover and/or stronger thermal stratification.

The size of diatom frustules in lake sediment could be a useful indicator of macroecological and macroevolutionary change in the diatom community in response to a lake's trophic status over time, if there are strong relationships between the limiting nutrient concentrations in a lake and the size structure of diatom assemblages deposited in lake sediments. To test the hypothesis that lake nutrient status influences the size structure of diatom assemblages, and to determine the direction of size change in response to a lake's trophic status, we quantified the size of diatom valves from the sediment surface of lakes characterized by a range of nutrient concentrations. To compare the effect of nutrient availability, as opposed to climate-induced stratification, we examined diatom community size structure from a contemporaneous set of shallow alkaline lakes (most had a mean depth < 10 m and volume $< 1 \times 10^8$ m^3). The goal of this study is to determine whether there are robust patterns in the size structure of plankton communities in response to phosphorus concentrations in lakes.

2. MATERIAL AND METHODS
(a) *Sampling*
Twenty-eight southeastern Ontario (Canada) lakes were chosen from a larger surface sediment calibration set assembled by Reavie & Smol (2001), which covered a large range of TP concentrations (summer: 0.002–0.032 mg l^{-1}). All the lakes were purposely chosen to be intermediate in volume (2.7–237 $\times 10^6$ m^3) and alkaline (summer pH: 7.3–8.6), so as to avoid any complicating factors arising from acidic lakes. Detailed information on the physical characteristics of the lakes, water quality and sediment sampling, water chemistry measurements and diatom slide preparation can be found in Reavie & Smol (2001). A subset of the information is provided in table 1. Lake sediments were sampled for diatoms as close as possible to their maximum depth, and the top 1 cm surface section was used for diatom slide preparation, using standard palaeolimnological procedures for surface sediment analyses (Smol 2008). The top centimetre of sediment provides a time-integrated sample of the diatom community composition over the last season to several years in the lake, and will vary somewhat between the lakes (Reavie & Smol 2001; Smol 2008). It is assumed that the point measurements of water quality provide a useful rank estimate of differences in nutrient status in these lakes over this time period (Reavie & Smol 2001; Reavie *et al.* 2002; Smol 2008). Homogenized wet surface sediment was weighed (approx. 0.5 g), then digested with a 50 : 50 mixture of nitric and sulphuric acid at 80°C for 1 h, then repeatedly washed to remove all acid, and then dried on cover-slips and mounted with Naphrax on glass slides (Battarbee *et al.* 2001).

Table 1. List of lakes in the study and associated maximum lake depth and Secchi depth, total summer phosphorus concentration and chlorophyll *a* concentration, and the size of the diatoms in the lake (75th percentile of log area, μm^2) for the whole diatom assemblage (all diatoms), and separated into planktonic, periphytic and benthic diatom communities.

lake	depth (m)	Secchi depth (m)	total P (mg l^{-1})	chl *a* (mg l^{-1})	75th percentile log area			
					all diatoms	planktonic	periphytic	benthic
anstruther	39.0	4.8	0.004	1.0	2.29	2.31	1.79	1.36
balsam	15.0	4.7	0.012	1.6	2.08	2.19	2.39	1.34
big clear	18.3	3.9	0.008	1.0	2.20	2.25	n.a.	1.49
big gull	26.0	4.5	0.008	2.6	1.99	1.99	n.a.	1.20
burridge	16.2	6.1	0.008	0.8	1.85	1.89	2.23	1.58
charleston	91.0	4.8	0.016	1.8	2.04	2.05	2.49	0.93
collins	10.1	2.6	0.026	3.4	1.54	1.77	2.01	1.47
crystal	33.0	4.9	0.008	1.0	2.06	2.06	2.10	1.19
dog	49.7	2.2	0.028	2.4	1.88	1.87	n.a.	1.29
farren	21.3	5.5	0.012	0.6	1.93	1.94	n.a.	1.14
gananoque	23.8	4.1	0.020	2.2	1.97	1.97	2.42	1.04
gilmour bay	25.0	5.1	0.010	1.2	2.09	2.11	n.a.	1.30
gould	61.6	6.0	0.010	1.2	1.85	1.88	n.a.	1.31
grippen	16.0	2.9	0.020	8.4	1.75	1.75	2.21	2.45
hambly	14.6	3.8	0.016	8.2	2.16	2.16	n.a.	1.40
inverary	6.5	2.2	0.022	7.8	1.98	1.99	n.a.	1.38
kashwakamak	21.9	4.9	0.006	0.6	2.00	2.02	2.16	1.51
limerick	29.0	5.3	0.006	0.8	2.20	2.22	2.31	1.55
mississagua	37.0	4.1	0.004	1.2	2.48	2.53	2.61	1.41
newboro	23.8	4.5	0.010	3.8	2.00	2.00	n.a.	2.14
red horse	37.0	3.4	0.016	4.0	2.01	2.02	n.a.	n.a.
round	32.0	6.9	0.004	1.0	2.57	2.58	2.96	1.18
sand	14.3	3.7	0.014	1.6	2.02	2.04	2.30	1.39
sharbot	31.0	4.4	0.002	1.4	2.08	2.14	2.35	1.26
skootamatta	25.3	4.6	0.006	2.4	2.17	2.17	2.18	1.48
tallan	26.0	6.0	0.008	0.8	2.31	2.35	2.00	1.34
troy	5.2	1.0	0.022	2.0	1.43	2.04	2.25	1.30
upper rideau	22.0	1.5	0.032	4.2	1.91	1.91	2.02	n.a.

(b) *Diatom data: size and taxonomy*

Diatoms were examined at $400\times$ magnification using a Zeiss Axioskop II with differential interference contrast imaging. The slide was scanned from the top left to bottom right; 438–583 images were taken of intact individual valves of the diatom frustules for each lake using a Canon PowerShot A640. To avoid double counting, frustules that did not lie entirely within the field of view were not measured or counted. The field of view was calibrated with a Zeiss micrometer and the area of each valve was determined using IMAGEJ (Abramoff *et al.* 2004); the pixel width was 0.45 and 0.11 μm for $10\times$ and $40\times$ objectives, respectively. Taxonomic identification followed methods and references provided by Reavie & Smol (2001). To ensure consistent taxonomic identification of all samples collected throughout the study, measurements from IMAGEJ were tabulated and used to crop each frustule image from the original source image. This table was repeatedly sorted by taxonomic identification, size and numerous morphometric characters, and inconsistencies were corrected in an effort to create an internally consistent database of observations. Diatoms identified to species were categorized as planktonic, benthic and/or periphytic using a combination of taxonomic references and expert knowledge (Krammer & Lange-Bertalot 1986–1991). The few observations not identified to species (<6% of the observations) were categorized with the planktonic species, the dominant category in these lakes.

Size measurements were made in both girdle view and valve view; genera such as *Aulacoseira* were most often in girdle view while many of the *Cyclotella* species were more frequently in valve view. To standardize measurements of *Cyclotella bodanica*, which was observed equally in girdle and valve view, the width in girdle view was used as an estimate of its valve diameter and the area of the valve was computed (π radius^2). Area was used as a measure of diatom size because this is what can be reliably measured when looking at a sample under a microscope. It can be difficult to obtain all the dimensions required to estimate volume; in general, the largest axial dimension is highly correlated to cell volume (Snoeijs *et al.* 2002).

(c) *Data analysis*

A minimum of 438 intact valves were photographed, identified and measured for each lake. For cells in chains, the individual valves were measured and sized. Several precautions were taken to test for detection and sampling bias. Valves were identified and sized for several slides using both $10\times$ and $40\times$ objectives, with no detectable bias, although taxonomic identification became difficult under the lower magnification. Because larger taxa often tend to be less abundant, we needed to ensure that our estimates of valve size were not biased downwards by insufficient sampling. Rarefaction curves, examined to determine how quartiles of the log size distribution varied as a function of number of valves included in simulated subsamples, indicate that the estimate of log size quartiles varied by <2 per cent for a range of $n = 300$–500, indicating that increasing sample sizes above

300 had little effect on the estimates of the mean, median, 25th or 75th percentile of log area of the assemblages (not shown). Therefore, our minimum count of 438 valves should be sufficient to provide a good estimate of relative abundance for the most abundant cells, but infrequently occurring taxa (<10% of total abundance) can be expected to have poorly constrained relative abundances with relative errors more than 30 per cent (Buzas 1990).

(d) Statistics computed

The quartiles (25th, 50th and 75th percentiles) of the log area were used as summary statistics to characterize the size distribution of diatoms for each lake. Spearman's rank correlation (Pearson's correlation on data converted to ranks) was used to assess the observed relationships between the median, 25th percentile, 75th percentile of log area and selected environmental parameters across the sampled lakes. Many of the environmental conditions within the lakes are correlated with each other; therefore, partial correlations (Sokal & Rohlf 1994) were used to assess the effect of a third variable (maximum lake depth, Secchi depth, lake pH and total nitrogen and phosphorus concentrations) on the correlation between size and macronutrient concentration.

3. RESULTS

(a) Size of individual species and communities within and among lakes

The size of the diatom frustules of the 146 species identified range from 2.4 to 5900 μm^2. The largest diatom species observed was *Surirella elegans* and the smallest was *Fragilaria pinnata*. Most species exhibited a skewed lognormal distribution in mean frustule size. There are some differences in the mean size of different species between different lakes, but we found that this is normally due to differences in the number of observations between the lakes. The size distribution of diatom frustules for all observations from these southeastern Ontario lakes ($n=13\,836$) has a skewed lognormal distribution with a mean log area of 1.786 ± 0.004 μm^2, reported errors are 1 s.e. (median area: 61 μm^2) (figure 1). The size distributions of diatoms (μm^2) from each lake separately tend to exhibit approximately skewed lognormal distributions (data not shown). The median area of the diatom community ranges from 16 μm^2 in Troy Lake to 156 μm^2 in Round Lake. Based on the total size distribution of all the diatoms measured, four quartiles in log area (μm^2) are identified (1st quartile, 0.384–1.469; 2nd quartile, 1.469–1.783; 3rd quartile, 1.783–2.077; 4th quartile, 2.077–3.769). The proportion of diatoms within a lake that fall in the 4th quartile increases and in the 1st quartile decreases with increasing median diatom size within a lake. The shift in the median size of diatoms within a lake is a result of taxonomic turnover of many species. No single species accounts for the pattern observed, indicating size not taxonomic identity as the selected character. More dominant species (more than 1% of total observations) are found in the lowest quartile (*F. pinnata*, *Fragilaria construens*, *Cyclotella pseudostelligera*, *Achnanthes minima*, etc.) than in the largest quartile (e.g. *C. bodanica*). An increase in median area may indicate changes in cell volume or aspect ratio, but we found that the median aspect ratio of species in a lake (as estimated from the length/width of the smallest bounding rectangle
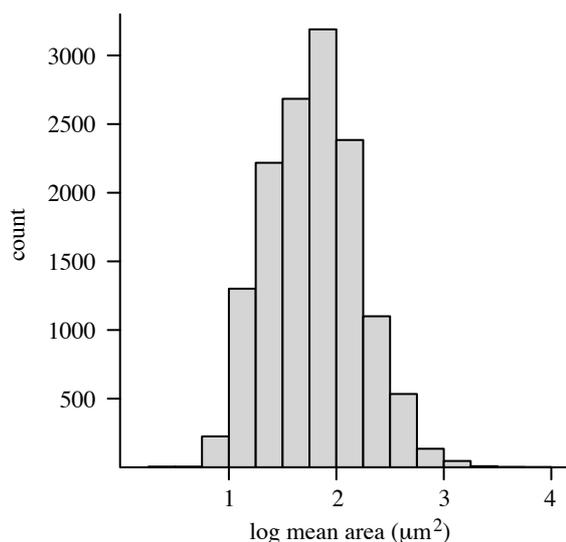
Figure 1. Frequency distribution of the size of diatoms in the lakes (area, μm^2), all lakes pooled ($n=13\,836$).

fit to the valve area) is not significantly related to the median size of diatoms in the lakes in this study (ANOVA, $n=28$, $p>0.38$).

(b) Size structure of diatom assemblages and relationship to environmental variables

Spring chlorophyll *a* is highly rank correlated with total spring phosphorus concentrations ($R=0.76$) and is negatively correlated with spring Secchi depths ($R=-0.92$), as expected. Molar nitrogen to phosphorus ratios all exceed 50:1, consistent with phosphorus-limited systems. Phosphorus is therefore the most likely limiting nutrient in the southeastern Ontario lakes examined. Chlorophyll *a* concentration is weakly correlated with the size of diatoms in the community (log 75th percentile of log valve area) in the lakes (rank correlation$=-0.28$, *p* value on ordinary least-squares regression slope$=0.18$).

There are significant correlations between the size of the diatoms in a lake and total macronutrient concentrations (TP and nitrogen, mg l^{-1}), and Secchi depth (m), in both spring and summer (table 2; figures 2 and 3). The correlation between the TP concentrations is highest with the 75th percentile of log valve area, decreases with the median, and is lowest with the 25th percentile of log valve area, indicating it is predominantly the larger species that are responding to changes in nutrient concentration (table 2).

The relationship between size structure and environmental variables varies markedly between the planktonic, periphytic and benthic diatom communities. The planktonic diatoms are responsible for the strong correlation between the size structure of the total diatom community and total macronutrient concentrations; by contrast, the benthic and periphytic diatom communities exhibit weak and statistically insignificant relationships with TP and nitrogen concentrations, Secchi depth and lake depth, except for a single significant negative correlation between Secchi depth and 25th percentile of log area of the benthic diatom community (table 2).

Partial rank correlations were used to assess the relationships between the size structure of the planktonic diatoms (75th percentile of log area) and total

Table 2. Spearman's rank correlation between the size of the diatoms (μm^2) within a lake for the 75th percentile, median and 25th percentile of log area and selected environmental variables. Planktonic species dominated the diatom communities in all lakes; strictly benthic and periphytic species were present in 26 and 18 of the 28 lakes, respectively. Correlations significant at $p < 0.05$ are noted with an asterisk.

environmental parameters	all diatoms	planktonic	periphytic	benthic
75th percentile of log area				
TP ($mg\,l^{-1}$)	−0.70*	−0.67*	−0.21	0.08
total nitrogen ($mg\,l^{-1}$)	−0.70*	−0.72*	−0.31	0.04
Secchi depth (m)	0.43*	0.38*	0.08	−0.10
lake depth (m)	0.43*	0.30	0.19	−0.30
50th percentile of log area				
TP ($mg\,l^{-1}$)	−0.55*	−0.53*	−0.15	−0.02
total nitrogen ($mg\,l^{-1}$)	−0.55*	−0.63*	0.04	0.13
Secchi depth (m)	0.30	0.25	0.03	−0.17
lake depth (m)	0.34	0.10	0.23	−0.30
25th percentile of log area				
TP ($mg\,l^{-1}$)	−0.24	−0.31	−0.14	0.14
total nitrogen ($mg\,l^{-1}$)	−0.25	−0.34	−0.11	0.22
Secchi depth (m)	0.10	0.03	0.04	−0.40*
lake depth (m)	0.21	−0.07	0.24	−0.22

macronutrient concentrations, Secchi depth and additional environmental and lake morphometric parameters that might be important to size structure: maximum lake depth and summer pH. The partial rank correlations between planktonic diatom size and TP concentration when holding lake depth, Secchi depth, pH and total nitrogen constant are −0.63, −0.61, −0.69 and −0.26, respectively. Compared with the rank correlation between diatom size and TP concentration (−0.67), this indicates that only total nitrogen concentration has a noticeable effect on this correlation. The reverse partial correlations, holding TP constant, between diatom size and these environmental variables support this conclusion. The rank correlation between diatom size and lake depth was 0.30, while the partial correlation holding TP concentration constant (r_p) was only 0.04, and the corresponding results for Secchi depth ($r = 0.38$, $r_p = -0.12$) indicate that TP reduces the explanatory power of these variables to nearly nothing. It should be noted that such a correlation does not necessarily indicate that the correlation between Secchi depth and diatom size structure is not present, since the increase in macronutrient availability stimulates the increase in phytoplankton biomass, which causes the decrease in lake transparency. The rank correlation with pH ($r = -0.47$) and partial correlation controlling for TP ($r_p = -0.51$) indicate that there is little interaction between these variables. Finally, the rank correlation with total nitrogen concentration ($r = -0.72$) and partial correlation controlling for TP concentration ($r_p = -0.42$) indicate that the relationship between nitrogen and phosphorus is nearly symmetric: each is a good predictor but the correlation between these predictors influences the correlation with the planktonic diatom community size structure.

4. DISCUSSION

In many marine systems, a shift from small cells to large cells is associated with increases in nutrient availability (Chisholm 1992; Li 2002; Irwin *et al.* 2006). By contrast, in our set of intermediate-sized alkaline lakes, we find a decrease in the size of planktonic diatoms with increasing
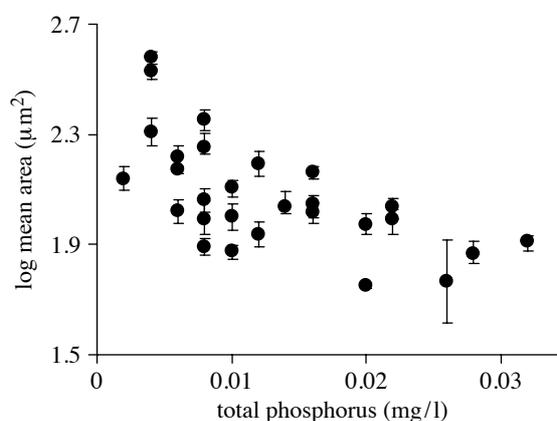

Figure 2. Size of the planktonic diatoms within the lakes (75th percentile of the log area, μm^2) with 95% bootstrapped confidence interval as a function of total summer phosphorus concentration ($mg\,l^{-1}$). Ordinary least-squares regression: $y = -19.6(\pm 4.5)x + 2.3$, $R = -0.65$, p value on slope = 0.0002, rank correlation coefficient = −0.7.

macronutrient concentration and decreasing lake transparency. The median and 75th percentile in the log area of the planktonic diatoms is negatively correlated with total macronutrient concentrations (figure 2) and positively correlated with lake transparency (Secchi depth; figure 3). By contrast, the periphytic and benthic diatom communities in the lakes exhibit no significant relationship between their size and macronutrient concentrations, consistent with some observations of periphyton communities in streams, creeks (Lavoie *et al.* 2006) and lakes (Cattaneo *et al.* 1997). Our results are consistent with the hypothesis that an increase in eutrophication can select for smaller and/or lighter planktonic (but not periphytic or benthic) diatoms with slower sinking rates owing to decreasing euphotic zone depths associated with nutrient-stimulated increases in chlorophyll concentrations, or other factors that decrease transparency in the upper water column (Smol *et al.* 1984; Huisman & Sommeijer 2002).

What accounts for the different diatom size responses to nutrient availability in these different aquatic systems? Why is an increase in phytoplankton or diatom size often
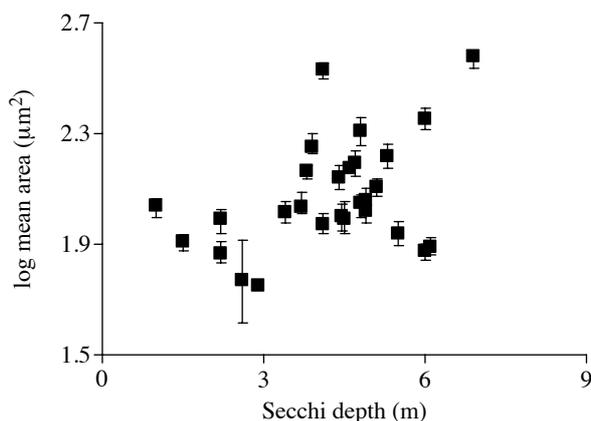
Figure 3. Size of the planktonic diatoms within the lakes (75th percentile of the log area, μm^2) with 95% bootstrapped confidence interval as a function of summer Secchi depth (m). Ordinary least-squares regression: $y = 0.098(\pm 0.027)x + 1.62$, $R = 0.58$, *p* value on slope $= 0.001$.

associated with higher surface water nutrient and chlorophyll concentrations in many oceanic systems while a more variable set of responses in the size structure of diatoms have been observed in rivers, streams and lakes? We hypothesize that the advantage of organism size under different environmental conditions may vary between different aquatic ecosystems owing to changes in the relative importance of size-dependent physiological and ecological processes under the different prevailing physical regimes. For example, in streams and creeks, where periphytic and benthic diatoms dominate, substrate variability, grazing and competition for resources are clearly more important than sinking rates in shaping community size structure (Passy 2007); furthermore, the temporally and spatially heterogeneous conditions that characterize these habitats may account for the lack of significant relationship between diatom size structure and TP concentration in these systems (Lavoie *et al.* 2006). In stratified oceanic systems and deeper lakes, such as Lake Tahoe (Winder *et al.* 2009), increases in stratification and nutrient limitation are often coupled, both favouring a decrease in cell size, which will act to increase nutrient diffusion, reduce nutrient requirements and reduce sinking rates. By contrast, nutrient concentration and supply rate can become somewhat uncoupled from stratification in aquatic systems impacted by significant external nutrient inputs, such as many North American small, shallow, inland lakes. These systems are often characterized by high chlorophyll *a* concentrations, sediment loads and/or coloured organic materials, which can contribute to shallow euphotic zone depths and light limitation of phytoplankton growth (Smol *et al.* 1984; Huisman & Sommeijer 2002). As a result, physiological and ecological strategies to avoid or reduce light limitation can become the primary determinants of the size structure of these phytoplankton communities.

Light limitation should select for smaller diatoms, which are less susceptible to light limitation due to their higher pigment-specific absorption efficiencies (Finkel 2001; Finkel *et al.* 2004) and lower sinking rates (Smayda 1970; Huisman & Sommeijer 2002), and which will tend to increase the proportion of the day they spend in the upper sunlit waters compared with larger diatoms (Smol *et al.* 1984). The southeastern Ontario lakes examined in this study have higher nutrient inputs and chlorophyll

a concentrations (0.6–8.4 mg m^{-3}) than typical oceanic systems (global average: 0.2–0.3 mg m^{-3}) or the oligotrophic Lake Tahoe (maximum concentration approx. 0.004 mg m^{-3}; Gregg & Conkright 2002; Winder *et al.* 2009), indicating that the size structure of the diatom communities in the small- and intermediate-sized southeastern Ontario lakes may have been primarily shaped by strategies to avoid light limitation. Observed increases in average phytoplankton cell size since 1995, associated with decreases in phosphate concentrations and increases in water column transparency in a coastal station in the North Sea (Wiltshire *et al.* 2008), suggest that light limitation may also shape phytoplankton size structure in some shallow coastal ocean systems. Feedbacks within the complex network of interactions in the food web—such as impacts on nutrient recycling and diatom growth, as well as competitive interactions between species and functional groups—make predictions of community size structure a continuing challenge (Perin *et al.* 1996; Attayde & Hannsson 2001). For example, competitive shifts in taxonomic composition of the community, such as an increase in large filamentous green algae under eutrophic conditions (Watson *et al.* 1997) or an increase in small diazotrophs under nitrogen-limiting conditions (regardless of the phosphate concentrations), can affect the relationship between the nutrient concentration and diatom size structure. Additional observations of both diatom and whole plankton community size structure in different oceanic and freshwater systems with a range of nutrient concentrations, water column transparency, mixing rates and trophic levels are required to address the current gaps in our knowledge.

There are robust patterns between the size structure of plankton communities and the environmental conditions characterizing different aquatic systems. In this study, we show that there is an increase in the proportion of larger planktonic diatoms in the community under lower nutrient concentrations and increased water column transparency. The change in diatom community size structure in these intermediate-sized lakes in response to the limiting nutrient concentrations differs from the predominant pattern seen in phytoplankton communities in frequently stratified marine and lake systems, which differs again from the more variable patterns reported in periphyton size structure in creeks and streams. We hypothesize that change in the relative importance of size-dependent processes (such as growth rate, nutrient uptake and requirements, light acquisition and sinking) may be responsible for the differences in the size structure of diatom assemblages in response to increases in limiting nutrient concentration. Using an ecophysiological framework, we hypothesize that the relative proportion of larger phytoplankton cells in a community will increase with nutrient concentration in systems where nutrient availability limits phytoplankton growth and standing stock, while increases in stratification and decreases in nutrient availability will tend to reduce cell size. By contrast, in aquatic systems, where nutrient concentration does not control phytoplankton growth and chlorophyll biomass is high, we predict a decrease in the relative proportion of larger phytoplankton cells with increasing nutrient concentration owing to decreases in euphotic zone depth and increased light limitation. In these systems, we predict that decreases in water column stratification will tend to

reduce the advantage of a reduced sinking rate, reducing or eliminating any change in community size structure with nutrient availability. Regardless of the cause, the presence and potential predictability of pattern suggests that diatom size may be a useful indicator for reconstructing past environmental conditions. Once we have a better understanding of the causes and consequences of changes in phytoplankton size structure, we will be able to use the sediment record not only to reconstruct past changes in water quality and macronutrient concentrations, but also to provide insight into past food web interactions and biogeochemical cycling.

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