

# Zooplankton and the total phosphorus – chlorophyll *a* relationship: hierarchical Bayesian analysis of measurement error

Amy M. Kamarainen, Freya E. Rowland, Reinette Biggs, and Stephen R. Carpenter

**Abstract:** Zooplankton grazing is important in resolving residual variation around the total phosphorus – chlorophyll *a* relationship. In empirical studies, zooplankton body size is often a better predictor of residual variation than zooplankton biomass. We investigate whether higher measurement error associated with zooplankton biomass may explain its lower predictive ability. We collected five replicate zooplankton biomass samples in 19 lakes, allowing us to quantify measurement error in volumetric zooplankton biomass with greater precision than in previous studies. A hierarchical Bayesian model was used to assess the predictive ability of volumetric zooplankton biomass and mean individual zooplankton length, corrected for measurement error. We found consistent effects of total zooplankton biomass, but not zooplankton length, on chlorophyll *a*. This finding does not appear to be related to the higher precision with which total zooplankton biomass was measured in our study, but rather to ecological factors. Interlake variation outweighed the effects of measurement error in estimating the strength of relationships between zooplankton variables and chlorophyll *a*. Our findings therefore suggest that studies to estimate zooplankton effects on phytoplankton should allocate resources to study a larger range of lakes over different time periods than to process replicate samples to reduce measurement error.

**Résumé :** Le broutage du zooplancton est important pour expliquer la variation résiduelle autour de la relation phosphore total – chlorophylle *a*. Dans les études empiriques, la taille corporelle du zooplancton est souvent une meilleure variable prédictive de la variation résiduelle que ne l'est la biomasse zooplanctonique. Nous examinons si l'erreur de mesure plus élevée associée à la biomasse zooplanctonique peut expliquer son pouvoir de prédiction réduit. Nous avons récolté cinq échantillons répétés de biomasse du zooplancton dans 19 lacs, ce qui nous a permis d'évaluer l'erreur de mesure de la biomasse volumétrique du zooplancton avec plus de précision que les études antérieures. Un modèle hiérarchique bayésien a servi à évaluer le pouvoir de prédiction de la biomasse volumétrique et de la longueur individuelle moyenne du zooplancton, une fois l'erreur de mesure corrigée. Nous avons observé des effets convergents de la biomasse du zooplancton total, mais non de la longueur du zooplancton, sur la chlorophylle *a*. Ce résultat ne semble pas relié à la précision plus grande avec laquelle la biomasse du zooplancton total a été mesurée dans notre étude, mais plutôt à des facteurs écologiques. La variation entre les lacs a plus d'effet que les erreurs de mesure sur l'estimation de la force des relations entre les variables zooplanctoniques et la chlorophylle *a*. Nos résultats laissent donc croire que les travaux cherchant à estimer les effets du zooplancton sur le phytoplancton devraient allouer leurs ressources de préférence à l'étude d'une plus grande étendue de lacs à différentes périodes plutôt qu'à l'analyse d'échantillons répétés afin de réduire l'erreur de mesure.

[Traduit par la Rédaction]

## Introduction

Models predicting chlorophyll *a* (Chl *a*) from total phosphorus (TP) characterize an important empirical relationship in limnology and underlie current theories of aquatic ecosystem functioning (Sakamoto 1966; Dillon and Rigler 1974). Over orders of magnitude in concentration, TP explains much of the variability in Chl *a*. Nonetheless, the residual variation around this relationship is substantial, and researchers have sought additional variables to help explain differences in Chl *a* among lakes. Zooplankton grazers often

explain part of the residual variation, reflecting the effects of grazing and nutrient recycling by grazers on phytoplankton. Although researchers have not always found zooplankton effects, total zooplankton biomass (Currie et al. 1999) or zooplankton body size (length or an index of community size structure) (Pace 1984; Carpenter et al. 1991; Taylor and Carter 1997) explains some of the variation in Chl *a* in most cases. In empirical studies, zooplankton body size is often a better predictor than biomass (Pace 1984; Carpenter et al. 1991; Taylor and Carter 1997).

The superiority of zooplankton body size, versus biomass,

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as a predictor of Chl *a* is puzzling. Most theoretical models of plankton dynamics link biomasses through the functional response equation for grazing; if body sizes enter at all, they affect the parameters of the biomass-based equations. Empirical field studies show that grazing rates depend more strongly on total zooplankton biomass than on body size (Cyr and Pace 1992), and mass-specific grazing rates decline with body size (Peters and Downing 1984). Therefore one would expect biomass to be the better predictor of Chl *a*. Several factors have been proposed to explain strong effects of body size. Greater diet breadth may enable larger zooplankters to consume a wider range of phytoplankton (Gliwicz 1980), but this relationship between diet breadth and zooplankton size depends on taxonomic composition of the zooplankton community (Cyr and Curtis 1999). Larger-bodied zooplankters have higher phosphorus demand and may exacerbate nutrient limitation of phytoplankton through sedimentation or excretion at relatively high N–P ratios (Elser et al. 1988; Sterner and Elser 2002). Finally, the rapid numerical response of large-bodied cladocerans may enable them to keep pace with blooming phytoplankton, at least temporarily (Carpenter et al. 2001). Yet there is another hypothesis — measurement error — that has not been investigated.

Measurement error in predictor variables causes regression analyses to underestimate the slope of the relationship between two variables and thereby underestimate the impact of a predictor that is measured with error (Fig. 1). Measurement error refers to imprecise observation of the true variable of interest. For example, measurement error can be caused by imprecise measuring instruments, by use of surrogate variables to represent the true variables of interest, or from sampling error when, for instance, the true variable of interest is the mean of some ecosystem attribute that is imprecisely estimated. It is well known that measurement error in predictors can have substantial effects on regression results (Fuller 1987; Carroll et al. 2006). Total volumetric zooplankton biomass and mean individual body size are typically measured with different degrees of precision in different studies, and these differences could potentially explain disparate conclusions about the best-fitting model for predicting chlorophyll *a*. We investigate this idea.

The relationship between chlorophyll *a*, phosphorus, and zooplankton is typically analyzed using classic linear regression, an approach that accounts for measurement error in the response variable (Chl *a*) but assumes that variation in predictor variables (e.g., nutrients and zooplankton) is derived from natural processes and that predictor variables are measured without error (Hanson and Peters 1984; Pace 1984; Carpenter et al. 1991). In exploring most ecological relationships, both predictor and response variables are measured with error. If measurement error in predictors is not corrected for in simple linear regression, it leads to attenuation (bias toward zero) of the estimated regression coefficients (Fuller 1987; Carroll et al. 1995; Gustafson 2004) (Fig. 1). The effects of measurement error are worsened in multiple linear regression models. Where two or more correlated predictors are present, and these predictors are measured with different levels of precision, attenuation of the less precisely measured predictor is exaggerated, whereas the coefficient

of the more precisely measured predictor becomes inflated (Fuller 1987; Carroll et al. 1995; Gustafson 2004).

In multiple linear regression models of the Chl *a*, TP, zooplankton relationship, TP and zooplankton size and biomass tend to be highly correlated. Additionally, TP and mean individual zooplankton size are measured with relatively high precision (often three replicate TP samples are collected and 20–100 individuals of each species are measured to derive an mean individual zooplankton size estimate per lake (Jeppesen et al. 2000)); total volumetric zooplankton biomass is measured with lower precision (a single composite volumetric estimate is often derived per lake, and at most, triplicate sample are collected) due to the cost of processing many replicate samples (Downing and Rigler 1984; Bird and Prairie 1985). We may therefore expect the TP and zooplankton size coefficients to be inflated, whereas the total zooplankton biomass coefficient may be attenuated. Observed differences in predictive power between zooplankton size and total zooplankton biomass may therefore be a statistical artifact rather than have an ecological basis.

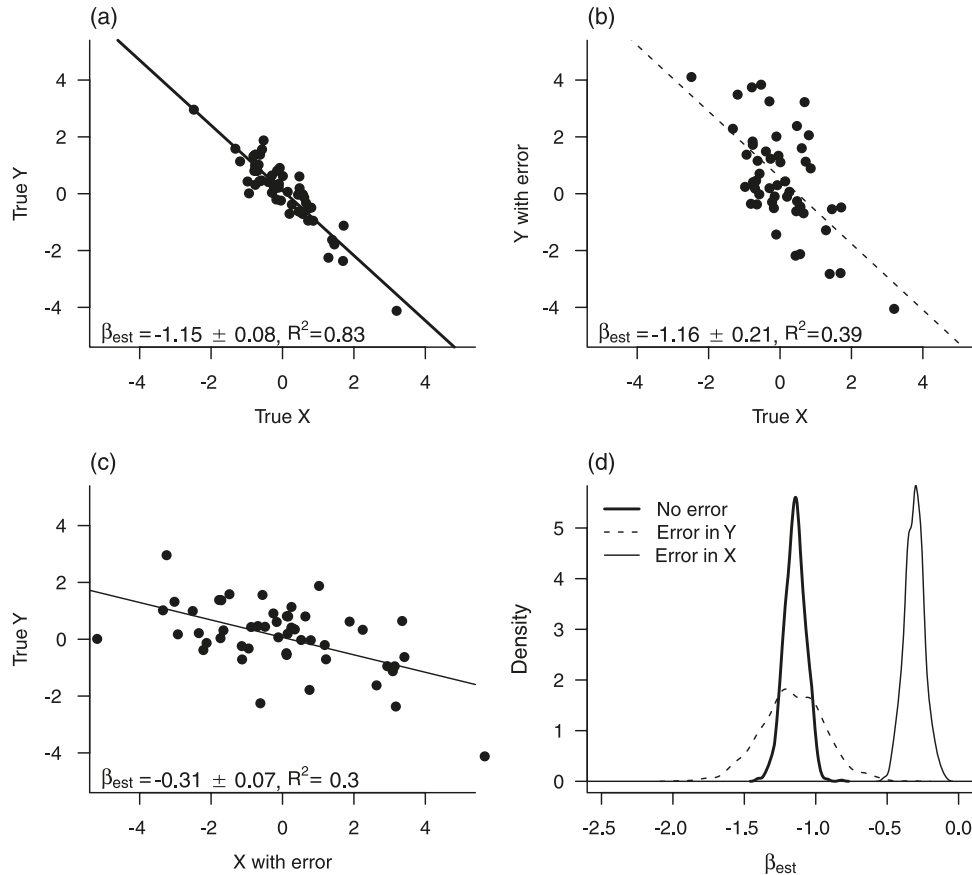
The aim of this study was to investigate whether differences in measurement error could explain the apparent weakness of total volumetric zooplankton biomass, in comparison with mean individual zooplankton size, as a predictor of Chl *a*. Zooplankton biomass may be a weak predictor, relative to mean individual zooplankton length, because zooplankton biomass usually has higher measurement error, relative to zooplankton length, that is not accounted for in classical regression analyses. To explore this idea, we quantified and corrected for measurement error in total volumetric zooplankton biomass and mean individual zooplankton length in a diverse set of lakes. Measurement error can be quantified through replication of field measurements. A unique contribution of this study is that we sampled total volumetric zooplankton biomass more intensively than is customary. Instead of a single tow, or several pooled tows, we collected five full replicate samples from each of 19 lakes. This rigorous replication allowed us to achieve a more precise estimate of measurement error compared with other studies. It follows that the coefficient for zooplankton biomass should be less attenuated when the data are analyzed using a method such as hierarchical Bayesian analysis that can account for measurement error in zooplankton biomass estimates. We used a hierarchical Bayesian model to correct for measurement error in our analyses because of two unique characteristics: (i) we were able to expand on a basic linear model to incorporate measurement error associated with predictor variables, and (ii) the hierarchical framework allowed for the simultaneous inclusion of variability within lakes and across lakes, as opposed to conventional approaches that focus on the across-lake scale. In our study, because we quantified measurement error in zooplankton biomass with greater precision and accounted for it using a hierarchical Bayesian model, we expected that total volumetric zooplankton biomass would be a stronger predictor of Chl *a* than mean individual zooplankton length.

## Materials and methods

### Study area

The study lakes are located in the Northern Highlands

**Fig. 1.** A simple linear regression model demonstrating the impact of measurement error on the strength of the estimated relationship  $\beta_{\text{est}}$  between the true  $X$  and  $Y$ . Measurement error in the response  $Y$  does not substantially affect the magnitude of  $\beta_{\text{est}}$ ; it simply increases the uncertainty about the estimate ( $b$  vs.  $a$ ). In contrast, measurement error in  $X$  substantially attenuates the strength of  $\beta_{\text{est}}$  between  $X$  and  $Y$  ( $c$  vs.  $a$ ). Changes in  $\beta_{\text{est}}$  are also apparent in histograms of  $\beta_{\text{est}}$  derived from a Bayesian analysis: measurement error in  $Y$  results in a flattening of the estimated distribution of  $\beta_{\text{est}}$ , whereas measurement error in  $X$  results in an underestimate of the true strength of the relationship between predictor and response ( $d$ ). Numbers in parentheses indicate two standard errors about  $\beta_{\text{est}}$ .



Lake District of Wisconsin, USA. Fourteen of the sample lakes are located in Vilas and Oneida County, Wisconsin, and five lakes lie in Gogebic County, Michigan, within the University of Notre Dame Environmental Research Center (Fig. 2). Lakes were chosen to represent a range of zooplankton sizes and chlorophyll  $a$  and total phosphorus concentrations. All lakes were sampled once between 30 May and 16 June of 2006 at central, deep-water locations.

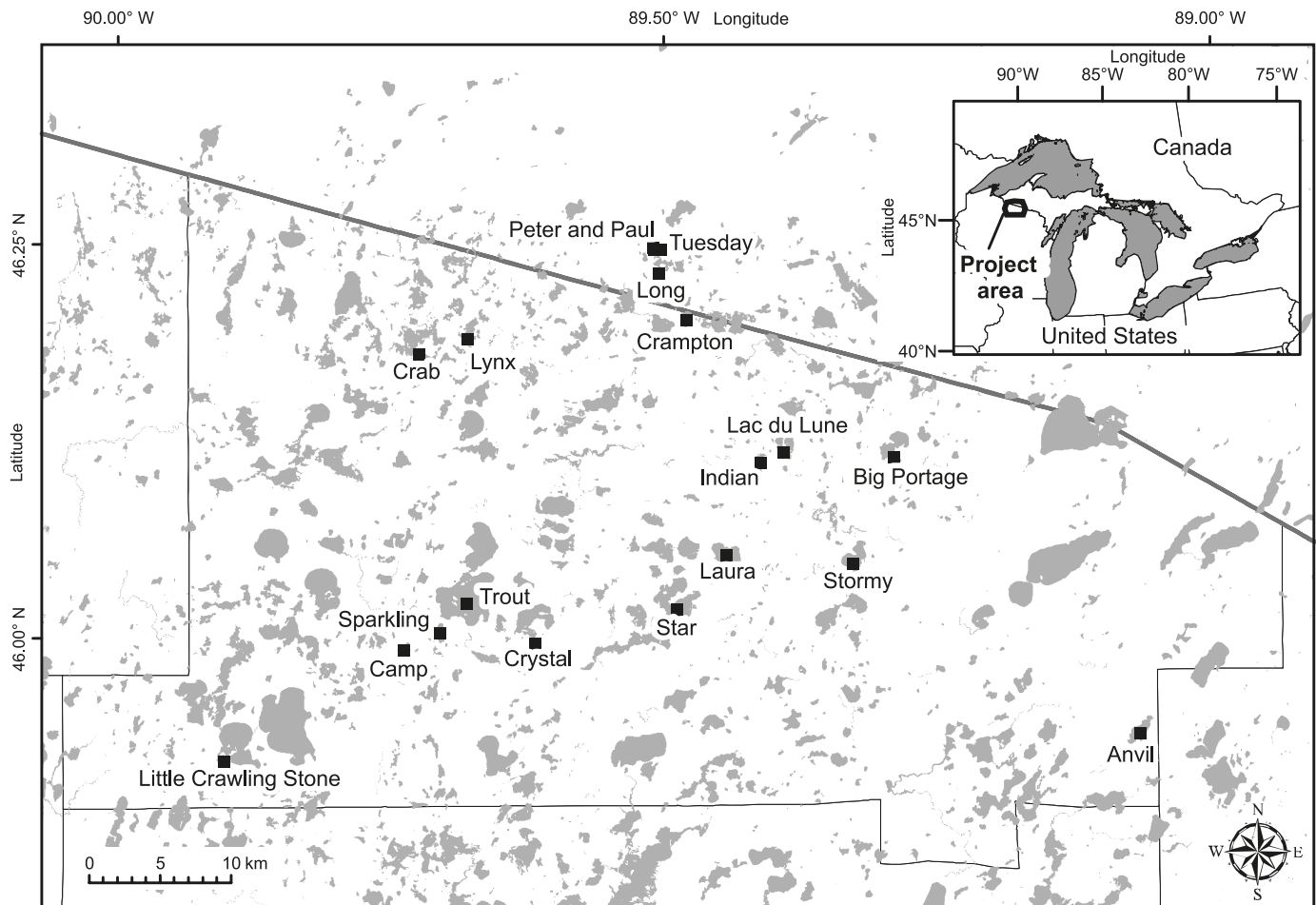
### Sampling

Chl  $a$  concentration was determined as a measurement of algal biomass. From each lake, six integrated samples were collected: three from the surface to the bottom of the epilimnion and three from the surface to the bottom of the metalimnion. Integrated samples were mixed in large opaque bottles and filtered in the field through glass fiber filters under low pressure using a peristaltic pump and inline filtration. Filters were frozen and later extracted in Optima methanol before fluorometric analysis according to US Environmental Protection Agency standard methods (Holm-Hansen and Riemann 1978; Arar et al. 1997). Measures were taken at each phase of Chl  $a$  analysis to avoid exposure to light. Final pigment concentrations were corrected for the influence of phaeopigments.

Whole-water samples for determination of TP were collected in acid-washed polyethylene bottles. Triplicate integrated samples were collected from the epilimnion. Discrete TP samples were collected from the middle of the metalimnion, the top of the hypolimnion, and 1 m above the bottom of the lake using a peristaltic pump. Samples were kept on ice until return to the lab and then preserved using Optima HCl. TP concentrations were analyzed using a Technicon Autoanalyzer following persulfate digestion (American Public Health Association, American Water Works Association, and Water Pollution Control Federation 1995).

We collected five zooplankton samples from each lake using vertical net hauls of a standard Wisconsin net with an anterior reducing cone (80  $\mu\text{m}$  Nitex mesh, 0.22 m diameter mouth). The net was lowered to 2–5 m above the lake bottom and raised at a speed of approximately 0.33  $\text{m}\cdot\text{s}^{-1}$ . Zooplankton were anesthetized and preserved in 70% ethanol. Assuming 100% efficiency of a Schindler–Patalas trap, the net efficiency of the Wisconsin net was determined to be approximately 66% based on samples from a single lake. We did not correct our volumetric zooplankton biomass values for net efficiency. If net efficiency is constant among lakes, it has no effect on variances of linear regression models.

**Fig. 2.** Map of lakes sampled in the Northern Highlands Lake District of Wisconsin, USA. All lakes lie within the coordinates 45°36' to 46°18'N and 89°00' to 89°54'W. Lake names are listed next to a solid square that indicates the lake location.



However, we did not test this assumption by measuring efficiencies in each individual lake.

### Zooplankton counting and biomass estimation

Each tow sample was drained through an 80  $\mu\text{m}$  mesh to remove all ethanol and then reconstituted to 50 mL with Milli-Q. The 50 mL sample was subsampled three times with a 1 mL Hensen–Stempel pipette. All crustacean zooplankton in each 1 mL subsample were counted, and up to 30 of each species or genus were measured to obtain species specific mean lengths. Total length measurements (excluding caudal rami and setae) were recorded for all copepods. All cladocerans except *Holopedium gibberum* were measured for total length of the carapace to the base of the spine. *Holopedium gibberum* lacks a rigid carapace, so the distance between setae natatores and the terminal claw of the postabdomen was chosen for measurement, as this part of the animal is more rigid and better represents the size of preserved specimens (Persson and Ekbohm 1980). The terminal claw of *H. gibberum* was measured at 50 $\times$  magnification to the nearest 0.02 mm, and all other zooplankton were measured at 25 $\times$  magnification to the nearest 0.04 mm using an ocular micrometer on a dissecting microscope.

All crustacean zooplankton were identified to genus, and in some cases, specimens were identified to the species

level. The genera identified include most *Daphnia* spp., *Bosmina* spp., *Ceriodaphnia* spp., *Chydorus* spp., *Diaptomus* spp., *Alona* spp., and *Acanthocyclops* spp. Those identified to species include *Daphnia pulex*, *Daphnia retrocurva*, *Diacyclops thomasi*, *Diaphanosoma birgei*, *Epischura lacustris*, *Eucyclops agilis*, *Holopedium gibberum*, *Leptodora kindtii*, *Mesocyclops edax*, and *Tropocyclops prasinus*. All copepod nauplii and copepodites that were too early in development to have defining adult characteristics were identified to the genus level.

Mean individual zooplankton length (ZL) for each lake was calculated by taking the weighted mean lengths of each species or genus across a sample and then averaging among the five samples to determine the mean individual zooplankton length within each lake. To estimate weight, mean lengths for each species or genus in each of the five samples were converted to mean dry weight estimates using published length – dry weight regressions (O'Brien and deNoyelles 1974; Dumont et al. 1975; Bottrell et al. 1976; Culver et al. 1985; Lawrence et al. 1987; Yan and Mackie 1987) (Appendix A, Table A1). Biomass for each genus or species was calculated by multiplying the density per litre by the estimated mean weight per individual. Genus- or species-specific biomass estimates were summed to get a volumetric estimate of biomass for each sample, and then

the five samples were averaged to get a grand mean biomass per lake. Therefore, zooplankton biomass (ZB) represents the total crustacean zooplankton biomass per volume of lake water ( $\mu\text{g dry weight}\cdot\text{L}^{-1}$ ).

### Data analysis

We used a hierarchical Bayesian modeling framework to assess the combined effects of TP, mean individual ZL, and total volumetric ZB on Chl *a* concentrations. We chose to use a hierarchical Bayesian framework as it allowed us to explicitly model the error in ZL and ZB measurements within each lake and account for this uncertainty in the estimated model parameters (Ellison 2004; Clark 2005). We carried out the analyses using the R2WinBUGS package (Sturtz et al. 2005) within the statistical software R (R Development Core Team 2007). (Code for the model can be found in Supplemental Appendix S1, available online from the NRC Data Depository.)<sup>3</sup>

The central process and parameters in which we were interested are given by the following linear model, based on observations from each lake (*i*):

$$(1) \quad \log(\text{Chl}a)_i = \beta_0 + \beta_1 \log(\text{TP})_i + \beta_2 \text{ZB}_i^T + \beta_3 \text{ZL}_i^T + \varepsilon_i$$

The Chl *a* and TP values in this model were taken as the average log-transformed concentrations in the epilimnion and metalimnion combined because this depth range encompassed the photic zone and best represented the characteristics of the water column over which the zooplankton tow was hauled. The average concentrations were calculated from the replicate measurements of Chl *a* and TP in each lake, and we used geometric means because the data were log-normally distributed. We assumed that these mean values represented the true mean Chl *a* and TP in each lake, measured with negligible error. The residual errors  $\varepsilon_i$  were assumed to be  $n(0, \sigma^2)$  distributed.

We explicitly modeled the measurement errors in ZL and ZB in each lake based on the five replicate tows (*j*) of the water column, assuming an additive measurement error model. For instance, for ZB, we assumed that the observed value in a particular tow  $\text{ZB}_{ij}$  reflected the true mean  $\text{ZB}_i^T$  plus measurement error  $u_i \sim n(0, v_i^2)$  in the particular lake:

$$\text{ZB}_{ij} = \text{ZB}_i^T + u_i$$

An analogous relationship was assumed for ZL. We modeled the measurement error in each lake separately because it varied substantially among lakes. We assessed the impact of correcting for measurement error by comparing the parameter estimates of a model based on a single tow with parameter estimates based on a model in which compilation of all five tows allowed us to estimate and correct for measurement error.

We used noninformative  $n(0, 100^2)$  priors for the regression parameters  $\beta_i$  and noninformative uniform densities  $u(0, 100)$  for the standard deviation parameters  $\sigma$  and  $v_i$ . As recommended by Gelman (2006) and Gelman and Hill (2007), we did not use inverse-gamma( $\alpha, \alpha$ ) prior distribu-

tions for the standard deviations as the resulting inferences are sensitive to  $\alpha$  when the standard deviations are close to zero.

### Results

Surveyed lakes covered a reasonable range in physical, chemical, and biological characteristics. Chl *a* concentration varied between 1.05 and 13.59  $\mu\text{g}\cdot\text{L}^{-1}$  (Table 1). TP and total nitrogen (TN) concentrations in the 19 lakes, averaged over the epilimnion and metalimnion, ranged from 7.6 to 21.6  $\mu\text{g}\cdot\text{L}^{-1}$  (Table 1) and from 223.1 to 493.6  $\mu\text{g}\cdot\text{L}^{-1}$ , respectively. Thus, the lakes sampled spanned a gradient from oligotrophic to mesotrophic. Morphometrics varied between the study lakes, with surface areas ranging from 1 to 1608 ha and maximum depths ranging from 7.9 to 35.7 m (Table 1). Morphometric characteristics were not related to TP or Chl *a* concentrations (Pearson's correlation,  $p > 0.10$  for Chl *a* and surface area, Chl *a* and maximum depth, TP and surface area, and TP and maximum depth). Although all of the lakes were deep enough to stratify, some were not completely stratified when samples were collected. There was no significant difference in mean Chl *a*, TP, ZL, or ZB between groups of lakes that were or were not stratified (Student's *t* test,  $p > 0.3$  in all cases).

We recorded 17 different genera or species of crustacean zooplankton in the 19 lakes. *Bosmina* spp., *Daphnia* spp., *Diacyclops thomasi*, *Diaptomus* spp., *Holopedium gibberum*, copepodites, and copepod nauplii most commonly dominated the zooplankton communities. In eight lakes, cladoceran biomass accounted for 50% or more of the total biomass, and 18 lakes had at least one *Daphnia* species present (Fig. 3). *Daphnia pulicaria*, the largest herbivorous zooplankton in these systems, were found in seven lakes and contributed significantly to the biomass estimates of Big Portage, Lake Laura, and Star Lake (52%, 73%, and 61%, respectively). At the other end of the spectrum, cladocerans made up less than 20% of the biomass in five lakes. The remaining six lakes had mixed crustacean zooplankton communities, including cyclopoid and calanoid copepods and cladocerans. Mean ZB varied considerably among lakes, ranging from 2.2 to 438.1  $\mu\text{g dry weight}\cdot\text{L}^{-1}$ , whereas mean length of the zooplankton community per lake ranged from 0.27 to 0.74 mm (Table 1). Taken together, these results indicate that sampled lakes represent a wide range in zooplankton biomass and community size structure.

We recorded substantial variability in Chl *a*, TP, ZB, and ZL both within and among lakes, as reported by the coefficient of variation (CV) in Table 1. The CV based on replicate measurements in each lake provides an estimate of the measurement error associated with each variable. It is notable that the CV, and hence estimated measurement errors, varied considerably from lake to lake. The range of CVs was smallest for ZL (1.2%–11.3%), followed by Chl *a* (1.1%–17.8%, except Anvil Lake (46%), which was identified as an outlier using Grubb's test). The CV ranges for TP and ZB were relatively large (2%–26% and 4%–35%, respectively). The CV of ZB was related to tow depth

<sup>3</sup>Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3858. For more information on obtaining material refer to [http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub\\_e.html](http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html).

**Table 1.** Morphometric characteristics and mean values of limnological variables for 19 lakes in Northern Wisconsin.

| Lake                  | Surface area (ha) | Maximum depth (m) | Tow depth (m) | Chl <i>a</i> * (µg·L <sup>-1</sup> ) | CV Chl <i>a</i> | TP <sup>†</sup> (µg·L <sup>-1</sup> ) | CV (TP) <sup>‡</sup> | ZL <sup>§</sup> (mm) | CV (ZL) | ZB <sup>  </sup> (µg dw·L <sup>-1</sup> ) | CV (ZB) |
|-----------------------|-------------------|-------------------|---------------|--------------------------------------|-----------------|---------------------------------------|----------------------|----------------------|---------|---|---------|
| Anvil                 | 154               | 9.8               | 6.0           | 4.05                                 | 0.467           | 16.47                                 | 0.021                | 0.38                 | 0.113   | 116.24                                    | 0.354   |
| Big Portage           | 258               | 12.2              | 7.0           | 1.84                                 | 0.051           | 10.93                                 | 0.208                | 0.44                 | 0.108   | 148.47                                    | 0.305   |
| Camp                  | 15                | 9.4               | 5.5           | 1.73                                 | 0.051           | 9.72                                  | 0.049                | 0.27                 | 0.035   | 25.63                                     | 0.109   |
| Crab                  | 384               | 18.3              | 13.0          | 5.53                                 | 0.173           | 12.63                                 | 0.169                | 0.51                 | 0.025   | 114.22                                    | 0.058   |
| Crampton              | 26                | 20.0              | 14.0          | 4.56                                 | 0.064           | 12.06                                 | 0.026                | 0.57                 | 0.069   | 89.21                                     | 0.041   |
| Crystal               | 37                | 20.4              | 15.0          | 1.48                                 | 0.043           | 9.57                                  | 0.105                | 0.54                 | 0.058   | 162.14                                    | 0.159   |
| Indian                | 161               | 7.9               | 5.0           | 2.59                                 | 0.039           | 17.29                                 | 0.090                | 0.52                 | 0.074   | 278.98                                    | 0.187   |
| Lac du Lune           | 172               | 20.7              | 14.0          | 1.82                                 | 0.020           | 9.88                                  | 0.019                | 0.47                 | 0.022   | 185.32                                    | 0.096   |
| Lake Laura            | 242               | 13.1              | 8.0           | 1.98                                 | 0.071           | 10.99                                 | 0.139                | 0.74                 | 0.037   | 128.86                                    | 0.220   |
| Little Crawling Stone | 43                | 13.4              | 10.0          | 4.28                                 | 0.025           | 15.12                                 | 0.091                | 0.41                 | 0.029   | 154.60                                    | 0.079   |
| Long Lake             | 6                 | 17.7              | 14.0          | 11.57                                | 0.045           | 21.64                                 | 0.099                | 0.34                 | 0.069   | 6.33                                      | 0.261   |
| Lynx Lake             | 137               | 14.6              | 9.0           | 3.14                                 | 0.011           | 9.28                                  | 0.115                | 0.55                 | 0.040   | 124.35                                    | 0.153   |
| Paul                  | 2                 | 15.0              | 9.0           | 8.46                                 | 0.144           | 21.14                                 | 0.142                | 0.37                 | 0.059   | 27.87                                     | 0.120   |
| Peter                 | 3                 | 19.3              | 14.0          | 12.16                                | 0.093           | 15.17                                 | 0.188                | 0.33                 | 0.030   | 23.53                                     | 0.142   |
| Sparkling             | 64                | 20.0              | 15.0          | 4.96                                 | 0.041           | 9.50                                  | 0.074                | 0.44                 | 0.012   | 105.74                                    | 0.036   |
| Star                  | 465               | 20.4              | 16.0          | 1.05                                 | 0.050           | 7.59                                  | 0.083                | 0.60                 | 0.062   | 177.51                                    | 0.076   |
| Stormy                | 211               | 19.2              | 14.0          | 1.21                                 | 0.071           | 8.25                                  | 0.260                | 0.50                 | 0.027   | 438.06                                    | 0.073   |
| Trout                 | 1608              | 35.7              | 30.0          | 2.16                                 | 0.019           | 12.91                                 | 0.151                | 0.50                 | 0.025   | 122.89                                    | 0.079   |
| Tuesday               | 1                 | 16.5              | 12.0          | 13.59                                | 0.037           | 21.03                                 | 0.159                | 0.29                 | 0.017   | 2.18                                      | 0.136   |
| Average               | 210               | 17.0              | 12.1          | 4.64                                 | 0.080           | 13.22                                 | 0.115                | 0.46                 | 0.048   | 128.01                                    | 0.141   |
| CV among lakes        |                   |                   |               | 0.849                                |                 | 0.340                                 |                      | 0.254                |         | 0.806                                     |         |

\*Chl *a* values represent the epilimnion + metalimnion.

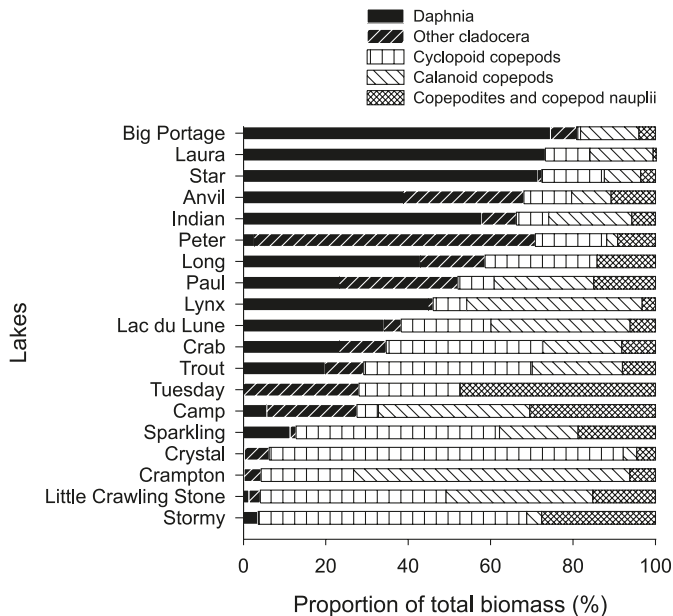
†TP (total phosphorus) values represent the epilimnion + metalimnion.

‡CV (TP) values are based on replicate samples in the epilimnion only. CV, coefficient of variation.

§Zooplankton length (ZL) is the weighted mean length per sample, averaged across replicates.

||Zooplankton biomass (ZB) is reported in dry weight (dw).

**Fig. 3.** Macrozooplankton community composition for 19 lakes in northern Wisconsin. The lakes are arranged vertically according to the relative abundance of cladoceran zooplankton.

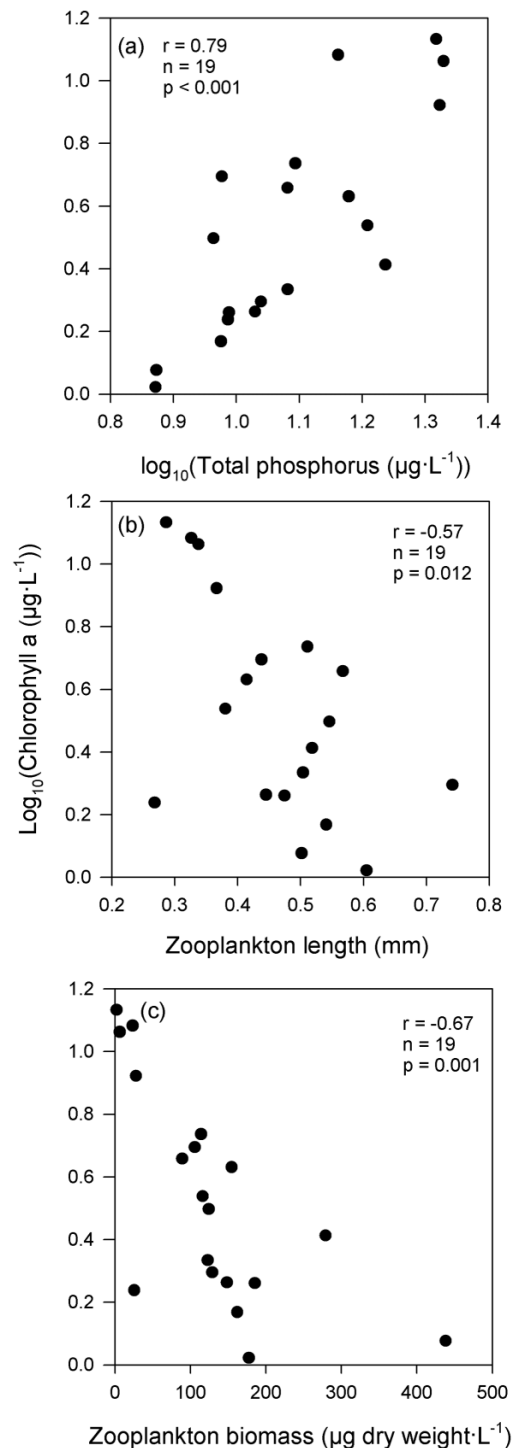


( $r = -0.47$ ,  $n = 19$ ,  $p = 0.041$ ) but did not appear related to lake surface area or in-lake biomass ( $r = -0.16$ ,  $p = 0.52$ , and  $r = -0.13$ ,  $p = 0.6$ , respectively).

The variables of interest in this study were significantly correlated with one another, as assessed by Pearson's correlation coefficient. As expected, there was a positive correlation between TP and Chl *a* ( $r = 0.79$ ,  $p < 0.001$ ; Fig. 4). Chl *a* was negatively correlated with ZB and ZL ( $r = -0.67$ ,  $p = 0.001$ , and  $r = -0.57$ ,  $p = 0.012$ , respectively; Fig. 4). TP was negatively correlated with both ZB and ZL ( $r = -0.529$ ,  $p = 0.021$ , and  $r = -0.517$ ,  $p = 0.023$ , respectively). The residuals of the TP–Chl *a* relationship showed a negative trend related to ZL ( $r = -0.25$ ,  $p = 0.296$ ) and ZB ( $r = -0.43$ ,  $p = 0.068$ ), though these correlations were not significant (Fig. 5). Additionally, ZL and ZB were positively correlated with one another ( $r = 0.486$ ,  $p = 0.035$ ). Although TP, ZB, and ZL co-vary, less than 30% of the variation in any given variable is explained by any other predictor.

Based on the hierarchical Bayesian model, correcting for measurement error, we found that TP and ZB were predictors of Chl *a* in our data set (Fig. 6). Bayesian credible intervals (95%) were calculated for each coefficient and those for TP ( $\beta_1$ ) and ZB ( $\beta_2$ ) did not overlap with zero ( $0.63 \leq \beta_1 \leq 2.31$  and  $-2.34 \leq \beta_2 \leq -0.08$ ). However, credible intervals for the ZL coefficient overlapped substantially with zero in both the full model (TP, ZB, and ZL) and a reduced model (TP and ZL only). This suggests that ZL had little or no effect on Chl *a* in our particular study. Analyses including surrogates or indices of zooplankton community size structure (mean length of cladocerans only, mean biomass per individual, percent of total biomass that is *Daphnia* spp.) were similarly not discernable from zero. The hierarchical Bayesian modeling approach returned qualitatively similar results to those produced by a traditional multiple linear regression analysis of the same data, but uncorrected for measurement error (Appendix B, Table B1). Therefore, the

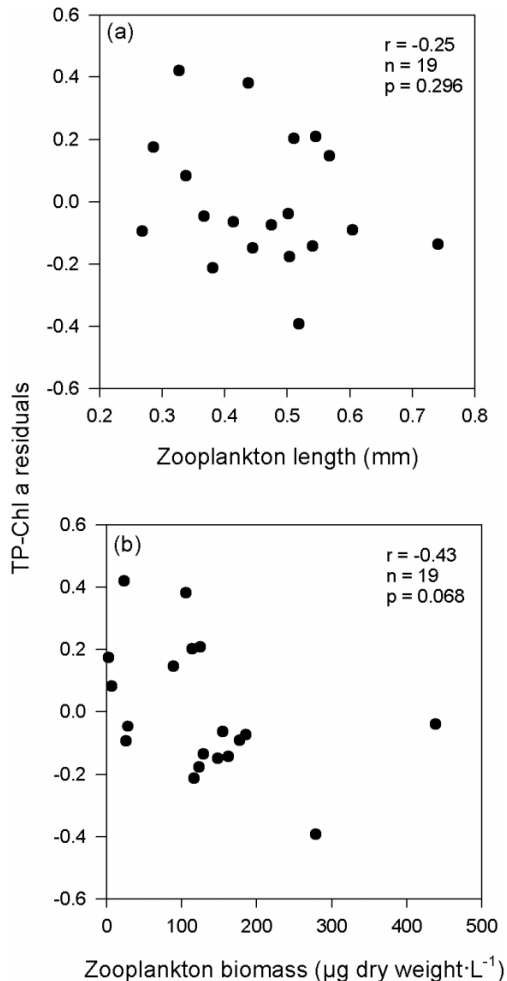
**Fig. 4.** Correlation between chlorophyll *a* and (a) total phosphorus (TP), (b) zooplankton length (ZL), and (c) zooplankton biomass (ZB) for northern Wisconsin lakes in late May and early June 2006.  $r$ , Pearson's correlation coefficient;  $n$ , sample size;  $p$ ,  $p$  value ( $\alpha = 0.05$ ).



presence of an effect of ZB and the weak effect of ZL are not explainable by measurement error but instead seem to reflect ecological patterns in the data.

We compared the full model (TP, ZB, and ZL) with a reduced model (TP and ZB only) using the deviance information criterion (DIC) (Spiegelhalter et al. 2002) and the

**Fig. 5.** Correlation between the residuals of the total phosphorus (TP) – Chl *a* relationship and (a) zooplankton length (ZL) and (b) zooplankton biomass (ZB). *r*, Pearson's correlation coefficient; *n*, sample size; *p*, *p* value ( $\alpha = 0.05$ ).



multilevel  $R^2$  (Gelman and Hill 2007). The DIC is a multilevel Bayesian analogue of the Akaike information criterion (AIC) (Akaike 1973) and is a measure of the fit of the model to the data corrected for the complexity of the model. The DIC for the full model was  $-980.8$ , and for the reduced model presented in Fig. 5, it was  $-557.6$ . The lower DIC for the full model suggests that it provides a better fit to the data. The corresponding multilevel  $R^2$  for the full and reduced models were 0.67 and 0.68, respectively. These statistics suggest that although the full model fits the data better, inclusion of ZL does not improve the explanatory power of the model. There is as yet no consensus about the best measures of fit for complex hierarchical models (Clark 2007), and current practice is to calculate several different measures (Gelman and Hill 2007), as done here.

We compared the regression coefficients of models based on a single tow, thus uncorrected for measurement error, with those based on all tows combined and corrected for measurement error (Fig. 7). The estimated coefficients (given in eq. 1) and the uncertainties around these estimates did not differ largely between tows, and neither did the estimates based on individual tows differ from estimates based

on the compilation of all five tows. As expected from measurement error theory, in the estimates derived from the individual tows (tow 1, 2, 3, 4, or 5), we observed a slight attenuating effect of measurement error on the estimated ZB coefficient ( $\beta_2$ ) and a corresponding slight inflation of the estimated TP coefficient ( $\beta_1$ ) compared with the estimates based on combining the data from all five tows and correcting for measurement error (All). However, these observed measurement error effects were small relative to the uncertainties about the estimated parameters (represented by the error bars in Fig. 7) resulting from the variability among lakes.

## Discussion

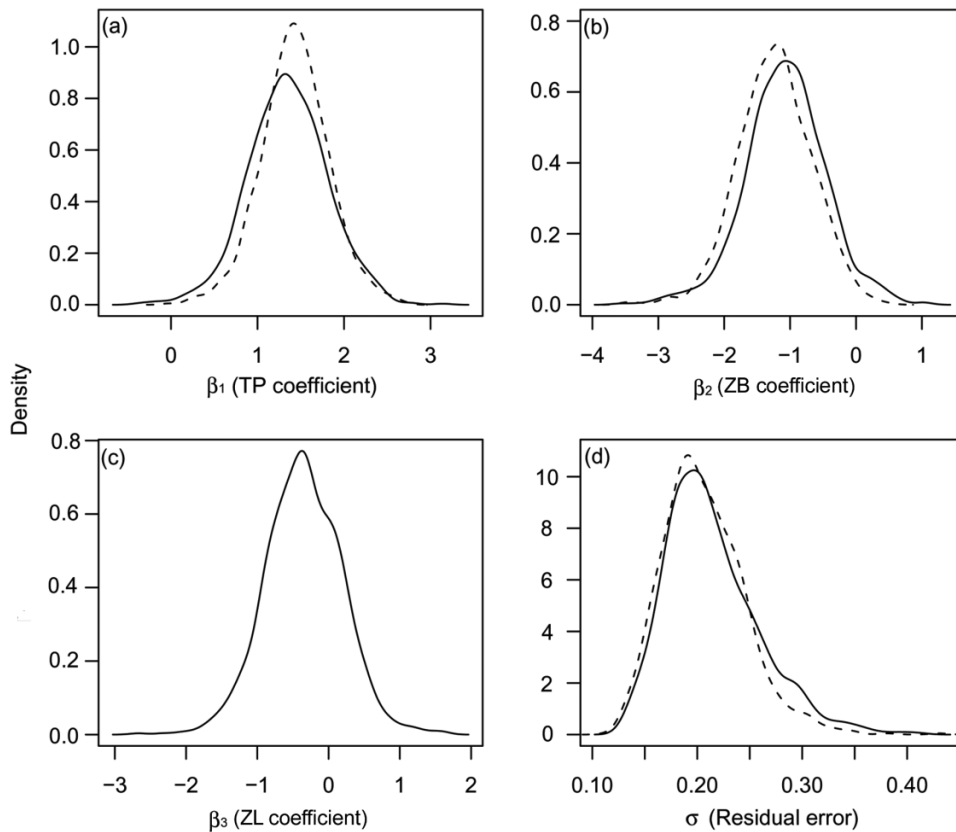
Two results from our study are notable: (i) in contrast to several earlier studies, we observed an effect of crustacean ZB, but not ZL, on Chl *a*, and (ii) this finding does not appear to be related to the higher precision with which crustacean ZB was measured in our study, but rather to ecological processes or variability.

Several studies have found that accounting for interlake differences in ZL improves estimates of Chl *a* (Pace 1984; Evans et al. 1996; Mazumder and Havens 1998). Cladoceran zooplankton, in particular *Daphnia* spp., are notably effective grazers in freshwater pelagic systems (Peters and Downing 1984; Carpenter et al. 1996; Steiner 2001), and low levels of Chl *a* are often associated with the presence of large cladocerans (Shapiro and Wright 1984; Carpenter et al. 2001). We observed a large range in mean cladoceran length per lake (0.24–1.40 mm) that was comparable with the range displayed by studies in which ZL was a significant predictor using conventional regression (Indian River lakes (0.5–1.7 mm); Pace 1984). Although we observed a large range in zooplankton size among lakes, the effect of ZL in our data set was weak.

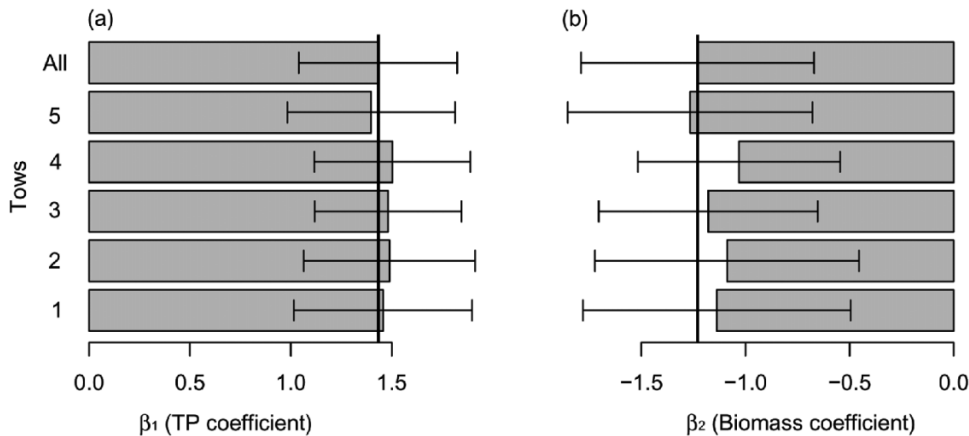
We found that indices related to zooplankton size (mean length of cladocerans only, mean biomass per individual, percentage of total biomass that is *Daphnia* spp.) also did not help explain the residual variation in Chl *a*. Because we focused on crustacean zooplankton and excluded rotifers and ciliates, the observed range of our zooplankton size indices may have been limited. We focused on crustacean zooplankton because these organisms make up the bulk of the zooplankton biomass in these lakes (Carpenter and Kitchell 1993) and seem to have the greatest effect on variability in Chl *a* within and among lakes (Carpenter et al. 1996). Pace (1984) measured both macro- and micro-zooplankton and derived an index of zooplankton community size based on the slope of the log–log relationships between zooplankton abundance and weight. The slopes of these lines were highly influenced by the inclusion of microzooplankton. The exclusion of microzooplankton from our study could potentially explain the lack of an observed effect using indices of zooplankton size.

Alternatively, Cyr (1998) showed that cladoceran- and copepod-dominated communities can maintain a similar effective grazing rate in low productivity systems. Many of our systems had reasonably low productivity, so it is possible that zooplankton community size structure did not influence total grazing pressure. This idea is further supported by

**Fig. 6.** Distribution of estimated coefficients for the hierarchical Bayesian model. The solid line represents a fit to the full model (including total phosphorus (TP), zooplankton biomass (ZB), and zooplankton length (ZL)); the dotted line represents a reduced model (including only TP and ZB).



**Fig. 7.** Estimates of (a) total phosphorus (TP) and (b) zooplankton biomass (ZB) coefficient based on the reduced model (TP and ZB predictors only) and data from each individual tow (1, 2, 3, 4, 5) (uncorrected for measurement error) compared with using all tows combined (All) (corrected for measurement error). The solid vertical line indicates the parameter estimate that has been corrected for measurement error based on the mean TP or ZB from the five replicate tows in each lake. Deviation of individual tows above (TP) and below (ZB) this line suggests inflation of the coefficients for the more precisely measured variable (TP) and attenuation of the coefficients for the less precisely measured variable (ZB). The error bars represent variation among lakes (one standard error).



a cross-lake study in which zooplankton community grazing rates were affected by zooplankton biomass, but not zooplankton size distribution (Cyr and Pace 1992).

In contrast to several earlier studies (Pace 1984; Jeppesen et al. 2000), we found that crustacean ZB rather than ZL

was a modest predictor of Chl *a* concentration in the lakes we sampled. Our study therefore suggests that in some contexts the zooplankton community can influence phytoplankton biomass independently of community size structure. Although ZB measurements are inherently imprecise

cise compared with measurements of ZL, our analyses do not suggest that our observation of a crustacean ZB effect was due to accounting for relative differences in measurement error. Regression coefficient estimates for crustacean ZB based on a single tow were only slightly attenuated compared with estimates based on the compilation of all five tows. Therefore, ZB was included as a predictor independent of the number of replicate tows included in the analysis.

The strength of the observed crustacean ZB relationship may vary over time because of the cyclic dynamics of the grazer–phytoplankton interaction (Carpenter and Kitchell 1987). We sampled single dates in early summer, whereas some other studies have used seasonal means to infer relationships. If dynamics of ZB and Chl *a* vary reciprocally over the summer, averaging over many dates may remove or obscure the dynamic relationship of ZB and Chl *a*. In such a case, short-term bottom-up and top-down dynamics that affect the biomass of the two communities may not be captured. This may not be the case for the ZL relationship if lakes with high ZL tend to have lower Chl *a* throughout the study period. Further research is needed to address the effects of averaging over time intervals of different lengths. Although time scale may affect the slope of the ZB–Chl *a* relationship (Carpenter and Kitchell 1987), our findings indicate that measurement error does not cause large bias in estimates of the slope from field data.

Our results do not support the hypothesis that measurement error weakens observed relationships of ZB to Chl *a*. Moreover, to better understand the drivers of phytoplankton biomass, it may be more important to sample a larger range of lakes over different time periods than to process replicate samples to reduce measurement error. Another compatible approach would be to collect a number of replicate samples per lake, but to pool these samples during the counting and measuring process. Such an approach would inherently capture much of the within-lake variation, yet eliminate the expenses associated with processing many individual replicate samples. Our study suggests that measurement error may not be an important bias, but we cannot infer that measurement error did not play a role in other studies that found zooplankton length and not biomass to be a significant predictor of Chl *a*. We could not test our hypothesis using data from previous studies because other studies collected fewer or no replicates and thus quantified measurement error with lower precision, preventing inclusion of these data in the hierarchical Bayesian model described here. Because we found that measurement error did not affect the results of this analysis, perhaps researchers should instead focus on other hypotheses that may affect zooplankton–Chl *a* relationships, such as diet breadth, numerical response, nutrient recycling, or other factors. Furthermore, our results suggest that studies of zooplankton–Chl *a* relationships should allocate limited research resources to sampling a wider range of drivers versus replication to correct for measurement error.

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## Appendices A and B

Appendices A and B follow.

## Appendix A

**Table A1.** Length – dry weight regressions applied to samples in the study with  $a$ ,  $b$ ,  $c$ , and  $d$  constants in  $\text{weight} = a \text{length}^b$  or  $\ln(\text{weight}) = c + d \ln(\text{length})$ , where weight is measured in micrograms and length is measured in millimetres.

| Species or genus                     | $a$     | $b$    | $c$    | $d$    | Source                      |
|--------------------------------------|---------|--------|--------|--------|-----------------------------|
| <i>Acanthocyclops</i> spp.           |         |        | 2.0577 | 2.5530 | Bottrell et al. 1976        |
| <i>Alona</i> spp.                    | 29.65   | 3.48   |        |        | Dumont et al. 1975          |
| <i>Bosmina</i> spp.                  | 17.7369 | 2.2291 |        |        | Culver et al. 1985          |
| <i>Ceriodaphnia</i>                  |         |        | 2.5623 | 3.3380 | Bottrell et al. 1976        |
| <i>Chydorus</i> spp.                 | 14.0793 | 1.9796 |        |        | Culver et al. 1985          |
| <i>Copepodites</i>                   |         |        | 2.0577 | 2.5530 | Bottrell et al. 1976        |
| <i>Copepod nauplii</i>               | 3.0093  | 1.7064 |        |        | Culver et al. 1985          |
| <i>Daphnia pulex</i> or <i>pulex</i> |         |        | 1.9445 | 2.72   | O'Brien and deNoyelles 1974 |
| <i>Daphnia retrocurva</i>            | 3.7847  | 2.6807 |        |        | Culver et al. 1985          |
| <i>Daphnia</i> spp.                  |         |        | 1.9445 | 2.72   | O'Brien and deNoyelles 1974 |
| <i>Diacyclops thomasi</i>            | 5.6713  | 1.9347 |        |        | Culver et al. 1985          |
| <i>Diaphanosoma birgei</i>           |         |        | 1.6242 | 3.0468 | Bottrell et al. 1976        |
| <i>Diaptomus</i> spp.                | 6.1927  | 1.9604 |        |        | Culver et al. 1985          |
| <i>Epischura lacustris</i>           |         |        | 1.467  | 2.4741 | Lawrence et al. 1987        |
| <i>Eucyclops agilis</i>              |         |        | 2.0577 | 2.5530 | Bottrell et al. 1976        |
| <i>Holopedium gibberum</i> *         |         |        | -17.08 | 3.52   | Yan and Mackie 1987         |
| <i>Leptodora kindtii</i>             | 1.5605  | 1.873  |        |        | Culver et al. 1985          |
| <i>Mesocyclops edax</i>              |         |        | 1.3472 | 3.0087 | Lawrence et al. 1987        |
| <i>Tropocyclops prasinus</i>         |         |        | 2.0577 | 2.5530 | Bottrell et al. 1976        |

\*The length measurement for *Holopedium gibberum* is the distance between setae natatores and the terminal claw of the postabdomen (in  $\mu\text{m}$ ). The equation to calculate total length was postabdominal claw length ( $\mu\text{m}$ ) = 191.64 total length (mm) + 37.00 (Yan and Mackie 1987).

## Appendix B

**Table B1.** Results of multiple linear regression analysis (not corrected for measurement error) predicting mean chlorophyll  $a$  concentrations from total phosphorus (TP), total volumetric zooplankton biomass (ZB), and mean individual zooplankton length (ZL).

|           | Coefficients | Standard error | $t$ statistic | $p$   |
|-----------|--------------|----------------|---------------|-------|
| Intercept | -0.646       | 0.570          | -1.135        | 0.274 |
| TP        | 1.345        | 0.399          | 3.372         | 0.004 |
| ZB        | -1.084       | 0.548          | -1.979        | 0.066 |
| ZL        | -0.334       | 0.474          | -0.704        | 0.492 |

Note:  $n = 19$ ,  $R^2 = 0.73$ ,  $p < 0.001$ .

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