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Light supply, plankton biomass, and seston stoichiometry in a gradient of lake mixing depths

Stella A. Berger,[1] *Sebastian Diehl, and Thomas J. Kunz*
Department Biologie II, Ludwig-Maximilians-Universität München, Grosshaderner Str. 2,
D-82152 Planegg-Martinsried, Germany

Dieter Albrecht
Max-Planck-Institut für Limnologie, August-Thienemann-Str. 2, D-24306 Plön, Germany

Amine M. Oucible and Sylvie Ritzer
Department Biologie II, Ludwig-Maximilians-Universität München, Grosshaderner Str. 2,
D-82152 Planegg-Martinsried, Germany

Abstract

We derive from a dynamic model that light availability, phytoplankton density, and the carbon : nutrient ratio of phytoplankton biomass should all be negatively related to mixed surface layer depth, whereas the areal standing stock of phytoplankton should show a unimodal, and total and dissolved nutrients a horizontal or increasing, relationship to mixing depth. These predictions agree closely with data from 65 central European lakes during summer stratification. In addition, zooplankton biomass was strongly negatively related to mixing depth in a subset of lakes. A decrease in mixing depth is thus a form of enrichment with light of the mixed surface layer, the effects of which could propagate to higher trophic levels.

The elemental composition of plants varies in response to the relative supplies with energy and materials (Rastetter et al. 1997; Sterner et al. 1997) and affects ecosystem processes such as the sequestration and storage of atmospheric carbon dioxide by living and dead plant biomass, the transfer of energy and matter along the food chain, and the storage and recycling of nutrients in ecosystems (Andersen 1997; Cebrian 1999; Hessen et al. 2004). Aquatic plants "compete" for light energy with abiotic absorbents such as water molecules, resulting in a steep decline of the light supply with water depth. As a consequence, specific production and the carbon : nutrient ratio of passively entrained planktonic producers are negatively affected by the vertical extension (=mixing depth) of the mixed water column (Sterner et al. 1997; Huisman 1999; Diehl et al. 2002). Mixing depth furthermore negatively affects volumetric nutrient supply to the surface layer from external sources (Diehl 2002) and the sinking loss rate of particulate nutrients to strata below the mixed surface layer (Visser et al. 1996; Ptacnik et al. 2003). Mixed layer depth can vary seasonally within lakes and geographically among lakes more than an order of magnitude (Guildford et al. 1994; Soto 2002; Kunz and Diehl 2003). Mixing depth is therefore expected to have important consequences for the dynamics of phytoplankton biomass, algal nutrient stoichiometry, light availability, nutrient supply, and nutrient retention in the mixed surface layer (Huisman and Weissing 1995; Diehl 2002; Diehl et al. 2005).

A decrease in mixing depth is a form of enrichment with light; that is, averaged over the mixed surface layer, the supply with light, an essential production-limiting resource, increases as mixing depth decreases (Diehl 2002). In analogy to the effects of enrichment with limiting nutrients, changes in mixing depth are therefore expected to propagate up the food chain. In freshwater lentic systems, numerous experimental and comparative studies have shown that the biomasses of pelagic herbivores and carnivores increase with nutrient enrichment (e.g., Persson et al. 1992; Hansson et al. 1998; Murdoch et al. 1998). In striking contrast to this wealth of nutrient enrichment studies, comparative studies relating the biomass of pelagic consumers to light supply are entirely lacking. Theoretical considerations and the few existing experimental studies suggest, however, that the relationship between light supply and consumer production might not be a monotonously positive one, but might be mediated by algal nutrient stoichiometry (Andersen et al. 2004). Specifically, if nutrient-deficient algae respond to increased light supply with a sufficiently strong increase in carbon production, the carbon-to-nutrient ratio of their biomass could increasingly deviate from the needs of their consumers. As a consequence, herbivores could become nutrient- rather than

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[1] Corresponding author (berger@zi.biologie.uni-muenchen.de).

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carbon-limited and respond negatively to increased light supply (Sterner et al. 1998; Urabe et al. 2002).

To our knowledge, the effect of mixing depth on the dynamics of light, nutrients, algal biomass, and seston stoichiometry in stratified water columns has not been comprehensively explored, either in theory or with empirical data. Here, we present a dynamic model that accounts for the mixing depth dependence of algal production and loss rates and for variability in algal nutrient stores. We derive predictions on how algal biomass and nutrient stoichiometry, as well as light levels and dissolved nutrient concentrations, should be affected by mixing depth and external nutrient supply, and we compare these predictions to the results of a survey of 65 central European lakes during summer stratification. Zooplankton is not yet included in the model. We did, however, sample zooplankton in a subset of the lakes and related its biomass to mixing depth and nutrient supply. Our results suggest that mixing depth is an important driver of the dynamics of light, nutrients, and algal biomass in the surface layer, the effects of which could propagate to at least the herbivore level.

Model

Structure—The model considers the well-mixed surface layer of a stratified water column and describes the dynamics of the concentrations of algal biomass, A (in units of carbon), and dissolved mineral nutrients, R, the nutrient content (quota) per algal biomass, Q, and the light intensity, $I(s)$, at depth s in the mixed layer.

$$\frac{dA}{dt} = \frac{A}{z}\int_0^z p(I(s), Q)ds - l_m A - \frac{v + D}{z}A \qquad (1)$$

$$\frac{dR}{dt} = \frac{D}{z}(R_{in} - R) - \rho(Q, R)A \qquad (2)$$

$$\frac{dQ}{dt} = \rho(Q, R) + l_m Q - \frac{Q}{z}\int_0^z p(I(s), Q)ds \qquad (3)$$

$$I(s) = I_{in}\, e^{-(kA + K_{bg})s} \qquad (4)$$

Specific algal growth rate (p) is assumed to be a multiplicative, saturating function of light intensity and nutrient quota (Droop 1974; Senft 1978), $p(I, Q) = p_{max}[I/(I + H)](1 - Q_{min}/Q)$, which averaged over a mixed water column of depth z yields Eq. 5.

$$\frac{1}{z}\int_0^z p[I(s), Q]ds = \frac{p_{max}}{kA + K_{bg}}\ln\left(\frac{H + I_{in}}{H + I_{out}}\right)\left(1 - \frac{Q_{min}}{Q}\right) \qquad (5)$$

Here, p_{max} is maximum specific production rate, Q_{min} is the algal nutrient quota at which growth ceases, k is the algal biomass-specific light attenuation coefficient, K_{bg} is the background light attenuation coefficient (describing attenuation by nonalgal components), and H is the half-saturation constant of light-dependent production. Light is treated as a single variable entering the water column with constant light intensity I_{in} (ignoring the complexities of spectral composition and temporal variation). Light intensity is assumed to decrease exponentially with depth (ignoring spectral differences in attenuation). Light intensity at the bottom of the mixed layer (Huisman and Weissing 1994), I_{out}, is defined by Eq. 4 for $s = z$ (z being mixing depth). Algae respire carbon at rate l_m and leave the mixed layer at rates proportional to their sinking velocity v and the water exchange rate D. Nutrients enter and leave the mixed layer at rate D and at concentrations R_{in} and R, respectively. Algal loss and nutrient exchange rates are inversely proportional to mixing depth z. Finally, nutrient uptake is a decreasing function of algal nutrient quota (Morel 1987) and a saturating function of external nutrient concentration (Eq. 6).

$$\rho(Q, R) = \rho_{max}\left(\frac{Q_{max} - Q}{Q_{max} - Q_{min}}\right)\frac{R}{M + R} \qquad (6)$$

Here, ρ_{max} is maximum specific nutrient uptake rate, M is the half-saturation constant of nutrient uptake, and Q_{max} is the algal nutrient quota at which nutrient uptake ceases. Algal nutrient quota increases through nutrient uptake and carbon respiration and decreases through growth.

Predictions—We explore how the model system responds to two environmental drivers—depth of the mixed water column and external nutrient supply—focusing on equilibrium conditions. We did not attempt a formal stability, but in numerical runs, the system always settled to a unique, globally stable equilibrium. We performed simulations in MATLAB (version 6.5) covering a range of plausible parameter values. The qualitative results described below have been observed in all of these simulations and will be illustrated with a few parameterized examples. Baseline parameter values and their units are listed in the caption of Fig. 1 and were chosen to reflect realistic, average algal traits (*see, e.g., chapter 3.5 in Andersen 1997*) and to roughly match environmental conditions in our study lakes during summer stratification.

At equilibrium, the model predicts that phytoplankton density and algal carbon : nutrient ratio are unimodally related to mixing depth (Fig. 1a,d) because algal carbon sequestration is limited by high sinking losses at the shallowest mixing depths and by low average light availability in deeply mixed layers. For realistic parameter values, both maxima occur, however, at very shallow mixing depths (<2 m; Fig. 1a,d), which are not normally observed over extended periods of time (*see* Web Appendix 1, http://www.aslo.org/lo/toc/vol_51/issue_4/1898a1.pdf). Thus, in the mixing depth range usually observed, we expect negative relationships of both phytoplankton density and the algal carbon : nutrient ratio to mixing depth (unshaded areas in Fig. 1). Note that inclusion of light inhibition in the phytoplankton production term (Eq. 5) would probably not greatly affect these predictions, because light inhibition is usually restricted to shallow

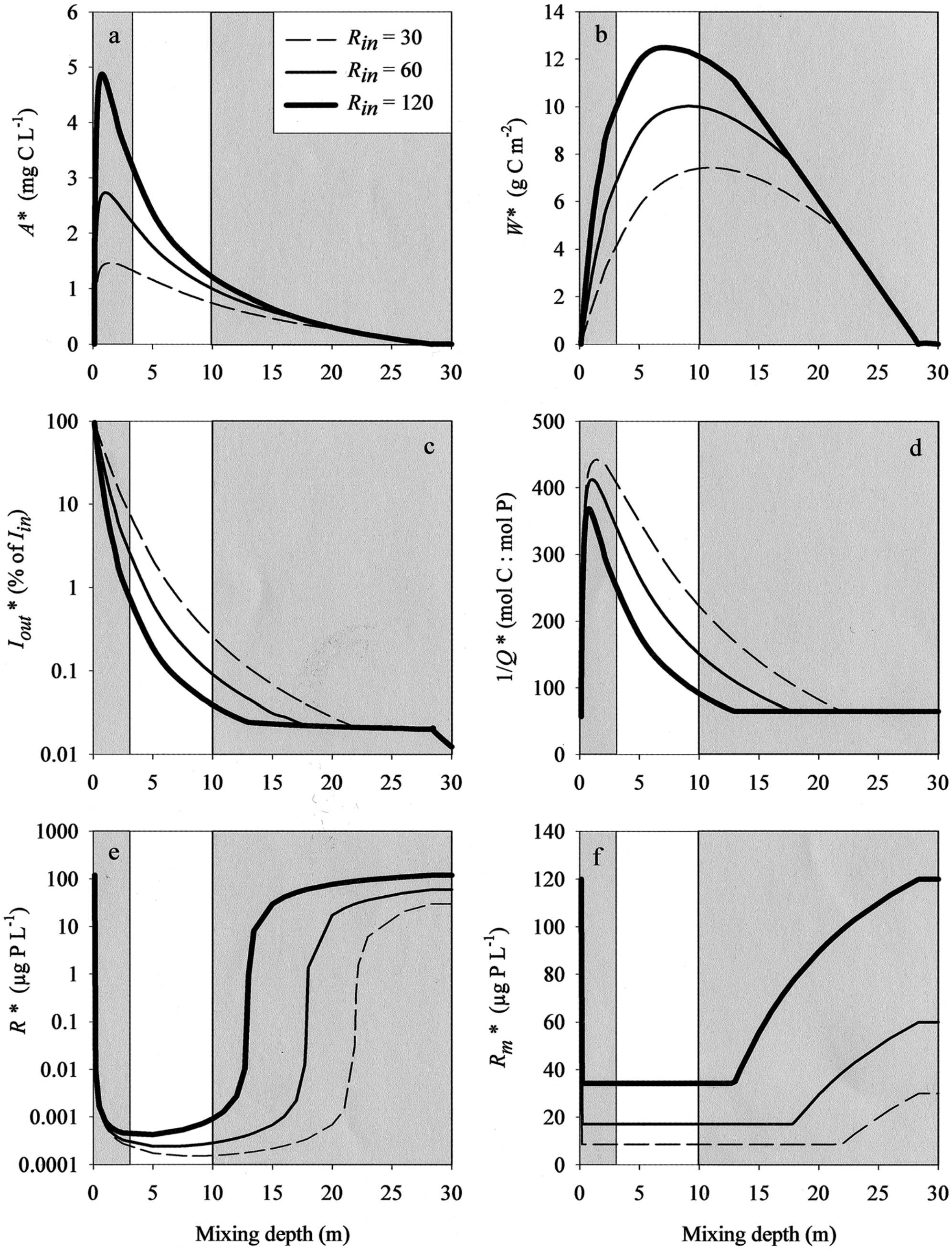

Fig. 1. Equilibrium relationships among mixing depth, nutrient supply, and six state variables predicted by the model. (a) Algal biomass concentration, A^*; (b) standing stock of algal biomass, W^*; (c) light at the bottom of the mixed layer, I_{out}^*; (d) carbon : nutrient ratio of algal biomass, $1/Q^*$; (e) dissolved mineral nutrient concentration, R^*; (f) total (dissolved + particulate) nutrient concentration, R_m^*. The illustrated examples are for realistic parameter values and three dissolved mineral phosphorus concentrations in the external source, R_{in}: 30 mg P m^{-3}, 60 mg P m^{-3}, and 120 mg P m^{-3}. The remaining parameter values are: $D = 0.02$ m d^{-1}, $H = 120$ µmol photons m^{-2} s^{-1}, $I_{in} = 300$ µmol photons m^{-2} s^{-1}, $k = 0.0004$ m^2 (mg^{-1} C)$^{-1}$, $K_{bg} = 0.3$ m^{-1}, $l_m = 0.13$ d^{-1}, $M = 1.5$ mg P m^{-3}, $p_{max} = 1.0$ d^{-1}, $Q_{max} = 0.04$ g P (g C)$^{-1}$, $Q_{min} = 0.004$ g P (g C)$^{-1}$, $\rho_{max} = 1$ g P (g C)$^{-1}$ d^{-1}, $v = 0.05$ m d^{-1}. Unshaded areas indicate the mixing depth range of the lake survey.

water depths. The areal standing stock of phytoplankton ($W = Az$, i.e., phytoplankton biomass summed over the mixed layer) is also unimodally related to mixing depth, but the maximum occurs in considerably deeper mixed layers (Fig. 1b) because, in shallow mixed layers, depth-integrated biomass is limited by the total amount of nutrients in the mixed water column (Huisman and Weissing 1995). Light intensity at the bottom of the mixed layer decreases with mixing depth (Fig. 1c). Finally, the concentration of the limiting nutrient in dissolved mineral form as well as total (dissolved plus particulate) nutrient concentration show flat-bottomed, U-shaped relationships to mixing depth, the decreasing limbs of which occur far below realistic mixing depths (<0.2 m; Fig. 1e,f). Thus, although nutrient supply rate is inversely related to mixing depth in the model, we expect both dissolved and total nutrients to be nearly independent of mixing depth across a mixing depth range typical of small to medium-sized lakes (unshaded areas in Fig. 1; note the logarithmic scale in Fig. 1e and that mineral nutrient concentrations dip three orders of magnitude below the detection level of 1 mg P m^{-3}). Within that range, essentially all nutrients are sequestered by algae, keeping dissolved nutrients at very low levels and leading to the predicted decrease in algal carbon : nutrient ratio with increasing mixing depth. Note that sinking losses depress total nutrient concentration considerably below the nutrient concentration in the external source (Fig. 1f). Once a threshold mixing depth is reached, algae become saturated with nutrients and cannot sequester all available nutrients (Fig. 1d). Beyond that, threshold algal biomass depends solely on light availability, and dissolved and total nutrients increase with mixing depth (Fig. 1b,e,f).

The model also predicts straightforward effects of nutrient supply: higher nutrient concentrations in the external supply lead to more phytoplankton biomass (except where algae are nutrient saturated, e.g., beyond mixing depth = 21 m in Fig. 1b,d), lower light levels, higher concentrations of total and dissolved nutrients, and a lower algal carbon : nutrient ratio (Fig. 1).

Materials and methods

Study lakes and sampling—To confront the model predictions with data, we sampled the surface layers of 65 central European lakes (area 0.03–80 km^2) several times during summer stratification and measured all state variables included in the model. For nutrients, we focused on phosphorus as the production-limiting nutrient in the majority of freshwater lakes (Hessen et al. 2004). Twenty-five lakes in southern Germany were sampled twice in 1998 (06–17 July, 16–28 September) and 40 lakes in northern Germany were sampled three times in 2001 (05–29 June, 12 July–03 August, 14 August–06 September). Lake characteristics are listed in Web Appendix 1. The lakes covered a moderate range of mixing depths (seasonal average 3.0–10.3 m) and a broad range of nutrient supply rates as inferred from total phosphorus (TP) concentrations (8–122 mg TP m^{-3}; *see* Web Appendix 1).

On each sampling occasion we first recorded a vertical profile of temperature, oxygen concentration, conductivity, and pH, and we measured photosynthetically active radiation (PAR) with a spherical underwater quantum sensor in 0.5-m steps down to the suspected lower limit of the mixed surface layer. Mixing depth (z) was defined as the depth at which the temperature difference to the lake surface did not exceed 1°C. We adopted this definition rather than more conventional definitions (e.g., the depth of the steepest thermal gradient) to avoid including water from the stratified metalimnion in our mixed layer samples. We then collected an integral water sample of the mixed surface layer. Depending on depth of the mixed layer, we took three to five 2-liter Ruttner samples at equidistant depths of the mixed layer (beginning at a depth of 0.5 m) and combined them into a single mixed sample. In 2001 we also collected a mixed layer zooplankton sample by hauling a 50-μm mesh net through the whole mixed surface layer.

Sample analyses—TP concentration was determined from unfiltered water samples. All other analyses were carried out on 200-μm filtered samples to exclude mesozooplankton. We determined soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) after filtration through membrane filters (0.45 μm) and TP after oxidation of all organic phosphorus according to the phosphorus–molybdate method. Particulate phosphorus was calculated as the difference between TP and TDP. After filtration of seston onto glass fiber filters (GF/C, Whatman), we determined chlorophyll *a* (Chl *a*) spectrophotometrically in 1998 and by high-performance liquid chromatography in 2001 and particulate organic carbon (POC) via combustion and infrared spectrometry. Microzooplankton was counted in preserved water samples with an inverted microscope. Mesozooplankton was counted and measured under a dissecting microscope. Total dry biomass of zooplankton (crustaceans + rotifers + ciliates) was calculated with taxon-specific estimates of individual mass for rotifers and ciliates and length–mass regressions for crustaceans (Botrell et al. 1976).

Comparison with model expectations: Statistical analyses—To compare lake data with equilibrium model expectations we used seasonal means averaged over the multiple samplings from each lake. We adopted this procedure to include each lake as a single, independent data point and to reduce the influence of sampling error and transient temporal variability within lakes. Although fluctuations in plankton biomass are often minor during summer stratification (Sommer et al. 1986), seasonal averages should more closely approach equilibrium conditions than would single measurements.

Because many model parameters (e.g., water exchange rate, background turbidity, algal sinking velocity, and physiological rates) were expected to vary among lakes but could not be assessed, we did not attempt a quantitative comparison between model expectations and lake data. Rather, we used stepwise multiple regression with backward elimination to ask whether the lake data matched the qualitative expectations described above (Fig. 1). Response variables included the volumetric density and areal standing stock of phytoplankton biomass (as Chl *a*), the SRP concentration, the seston carbon : phosphorus ratio, the intensity of PAR at the bottom of the mixed layer (I_{out} in percent of $I_{\text{in}} = 100 \times \exp[-Kz]$, where K is the slope of a linear regression of natural log–transformed PAR vs. depth), and the density of zooplankton (as dry mass). As predictor variables, we used mixing depth (z), squared mixing depth (z^2), TP, water temperature (Temp), and sampling region (north [N] vs. south [S] Germany).

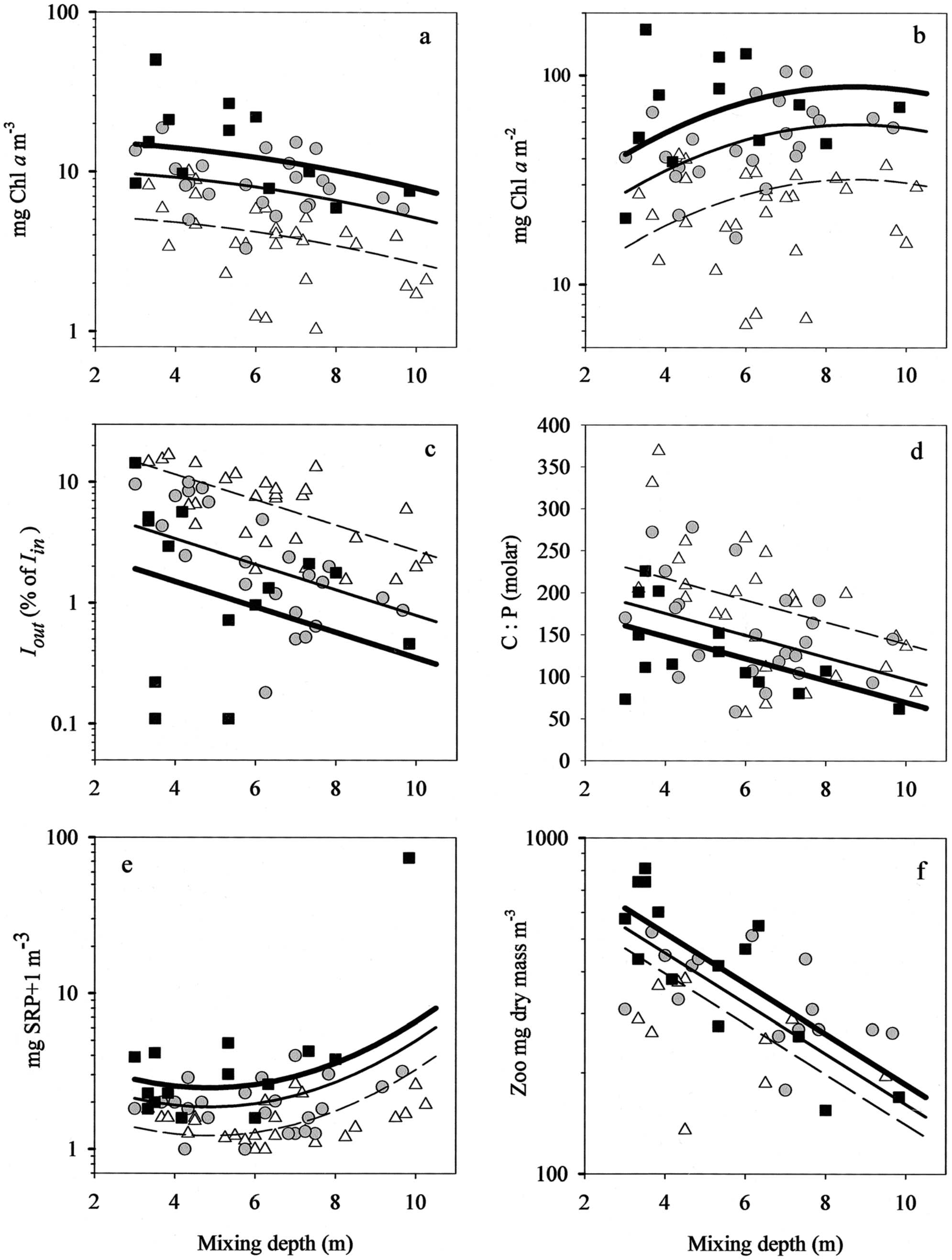

Fig. 2. Relationships among mixing depth, nutrient loading, and six variables in the surveyed lakes. (a) Algal biomass concentration (mg Chl *a* m^{-3}); (b) standing stock of algal biomass (mg Chl *a* m^{-2}); (c) intensity of photosynthetically active radiation at the bottom of the mixed layer (% of surface irradiation); (d) molar seston carbon : phosphorus (C : P) ratio; (e) dissolved mineral phosphorus concentration (mg [SRP + 1] m^{-3}); (f) zooplankton density (g dry mass m^{-3}). Nutrient loading is approximated by total phosphorus (TP) concentration, and lines illustrate the empirical regression models (Table 1) for the median TP values in three nutrient categories: TP < 20 mg m^{-3} (white triangles, dashed line), TP $= 20$–30 mg m^{-3} (gray circles, thin solid line), TP > 30 mg m^{-3} (black squares, thick solid line). $n = 65$ (panels a–e), $n = 40$ (panel f).

Predictor variables were included in the regression model at $p < 0.05$ and excluded at $p > 0.1$.

Strictly speaking, TP is not an independent variable but a response variable in our model. However, because data on external nutrient supply are difficult to obtain, TP is conventionally used as a proxy of phosphorus supply from external sources (Vollenweider 1976; Sterner et al. 1997). Our model actually gives a theoretical justification to this convention because it predicts a strong positive relationship between total nutrient concentration and external nutrient

Table 1. Relationships among response and predictor variables in the study lakes. Response variables are algal biomass concentration (mg Chl *a* m^{-3}), standing stock of algal biomass (mg Chl *a* m^{-2}), light at the bottom of the mixed layer (I_{out}, % incident PAR), seston C : P ratio (mol/mol), soluble reactive phosphorus concentration (mg SRP m^{-3}), and zooplankton density (Zoo, g dry mass m^{-3}). Predictor variables are total phosphorus concentration (TP, mg m^{-3}), mixing depth (z, m), squared mixing depth (z^2, m^2), water temperature (Temp, °C), and region (N vs. S Germany); $n = 40$ for zooplankton; $n = 65$ for all other variables.

Response variables	Regression equations with partial p-values					R^2	Variables excluded
Algal biomass concentration							
log Chl a =	−1.03	+ 0.95 log TP	$- 0.003z^2$	+ 0.049 Temp		0.79	z, region
		$p < 0.001$	$p = 0.005$	$p = 0.007$			
Standing stock of algal biomass							
log Chl a =	−1.16	+ 0.93 log TP	$+ 0.17z$	$- 0.010\ z^2$	+ 0.049Temp	0.73	region
		$p < 0.001$	$p = 0.016$	$p = 0.054$	$p = 0.002$		
Light at the bottom of the mixed layer							
log I_{out} =	2.16	− 1.79 log TP	$- 0.11\ z$	+ 0.072 Temp	± region*	0.65	z^2
		$p < 0.001$	$p < 0.001$	$p = 0.017$	$p < 0.001$		
Seston C : P ratio							
C : P =	201	− 141 log TP	$- 13.07\ z$	+ 12.50 Temp		0.39	z^2, region
		$p < 0.001$	$p = 0.002$	$p = 0.012$			
Dissolved nutrient concentration							
log(SRP + 1) =	−0.23	+ 0.62 log TP	$- 0.16\ z$	$+ 0.016\ z^2$		0.52	Temp, region
		$p < 0.001$	$p = 0.056$	$p = 0.012$			
Zooplankton biomass							
log Zoo =	3.61	+ 0.31 log TP	$- 0.075\ z$	− 0.058 Temp		0.51	z^2, region
		$p = 0.002$	$p < 0.001$	$p = 0.036$			

* Sign and value of regression coefficient not relevant because region was coded as a dummy variable.

supply, but no relationship between total nutrient concentration and mixing depth over large ranges of mixing depth (Fig. 1f). As predicted for the range of observed mixing depths, TP and z were indeed uncorrelated in the data (Pearson $r = -0.11$, $p > 0.1$). Because water temperature can directly influence phytoplankton (and zooplankton) growth rates, we included it as an additional variable in the regression analyses. Finally, because N and S German lakes differ in basin geology and were sampled in different years, we included Region (N vs. S) as a dummy variable.

Before analysis, zooplankton biomass, Chl *a*, I_{out}, SRP, and TP were log- or log(x + 1)-transformed and then averaged across multiple samplings. Studentized residuals of all dependent variables were normally distributed (Kolmogorov–Smirnov test $p > 0.05$) and there was only one outlier (Cook's $d > 1.0$), the SRP value of Lake Wittensee (Fig. 2e; Cook's $d = 1.99$).

Results

Generally, we found very good qualitative agreement between observed and predicted relationships among variables (compare Fig. 2 and Table 1 to unshaded areas in Fig. 1). Algal biomass concentration (as Chl *a*) was negatively related to mixing depth and positively related to TP concentration (Fig. 2a; Table 1). The areal standing stock of algal biomass was best described by a unimodal relationship with mixing depth (Table 1). Similar to the numerical example, the peak of the relationship occurred close to the highest observed mixing depths and was rather flat (Fig. 2b). Chl *a* : POC ratios were independent of mixing depth (linear regression, $R^2 = 0.01$, $p = 0.35$), suggesting that the increasing limb of the latter relationship in Fig. 2b was not an artifact of algal photoadaptation to darker environments at higher mixing depths. Light intensity at the bottom of the mixed layer (I_{out}) and the seston carbon : phosphorus ratio were negatively related to both mixing depth and TP (Fig. 2c,d; Table 1). The latter suggests that nutrient enrichment enhanced light attenuation by increasing phytoplankton density (Fig. 2a,c). Finally, the concentration of soluble reactive phosphorus was best fit by a positive relationship to TP and a U-shaped relationship to mixing depth (Table 1). Similar to the numerical example, the relationship was almost flat at low to intermediate mixing depths (Fig. 2e). Omitting the SRP value of Lake Wittensee (outlier in Fig. 2e; Cook's $d = 1.99$) leads to the exclusion of z and the inclusion of Region in the set of predictor variables but does not change the qualitative relationships of z^2 and TP to SRP.

A novel and striking finding was that zooplankton biomass, for which we have no model predictions, was strongly negatively related to mixing depth and positively related to TP (Fig. 2f; Table 1). Mean seasonal water temperature ranged from 13.5°C to 21.2°C. Although mixing depth and water temperature were negatively correlated (Pearson $r = -0.54$, $p < 0.001$), they were usually both retained in the regression models, suggesting that their contributions to the variance in response variables were largely independent.

Discussion

Our model extends similar strategic ecosystem models by Huisman and Weissing (1995) and Diehl (2002) to include flexible algal nutrient stoichiometry. Thus, the model comprehensively describes the relationships among phytoplankton biomass and carbon : nutrient stoichiometry, dissolved nutrients, light, and mixing depth. To our knowledge, our lake survey is the only available data set that reports all state variables described by the model. Given that factors unaccounted for by the model (e.g., algal taxonomic composition, zooplankton grazing) should have produced considerable noise in the lake data, the qualitative agreement between theoretical expectations and data is striking. Notably, we observed the predicted negative relationships of phytoplankton density and algal C : P ratio to mixing depth in spite of the rather limited range of mixing depths covered by our study. Nutrient supply explained, however, a relatively larger part of the variation in Chl *a* concentrations than did mixing depth (simple regressions of log Chl *a* vs. TP, vs. z, and vs. z^2 yield R^2 values of 0.69, 0.22, and 0.20, respectively). This is not surprising given that the TP–Chl *a* correlation is one of the most pervasive empirical patterns in limnology (Peters 1986). Our data suggest, however, that a substantial portion of the residuals from this relationship is explained by variation in mixing depth. We expect that the relative importance of light limitation should increase toward more deeply mixed systems. Strong negative effects of mixing depth on algal Chl *a* levels have indeed been reported from very deeply mixed lakes (Soto 2002) and from the ocean (Mitchell and Holm-Hansen 1991; Boyd 2002). It should be noted that in a fair proportion of our study lakes light levels should have been sufficient to support photosynthesis below the mixed surface layer. To get a more comprehensive understanding of the consequences of mixing depth for stratified water columns, future theoretical and empirical studies should therefore take deeper strata into consideration.

We found a positive relationship between zooplankton biomass and total phosphorus content in the 40 N German lakes. This finding merely corroborates a pattern described in several earlier studies (e.g., McCauley and Kalff 1981). Our study is, however, the first one to explore the relationship of zooplankton biomass density to mixing depth. We found a strong negative relationship between the two. The data thus strongly suggest that enrichment with either light or nutrients can both translate into enhanced secondary production within the range of environmental conditions covered by our study. Recent experiments have demonstrated that this need not always be the case. Increased light supply can actually cause herbivore biomass to decrease if increased carbon sequestration by primary producers is accompanied by a sufficiently strong decrease in plant quality (as manifested in an increased carbon-to-nutrient ratio of plant biomass; Urabe and Sterner 1996; Sterner et al. 1998; Urabe et al. 2002). In our lake data, seston C : P ratios did indeed increase toward shallower mixing depths. Still, with two exceptions, molar seston C : P ratios were always <300, the empirically estimated threshold for phosphorus limitation in the most phosphorus-demanding grazers such as *Daphnia* (Hessen 1992; Urabe and Watanabe 1992). Thus, although the relative contributions of carbon and nutrients to herbivore growth limitation are expected to vary with food density (Sterner 1997; Muller et al. 2001), our data suggest that severe phosphorus limitation of zooplankton was unlikely in the sampled, relatively nutrient-rich, N German lakes and that, consequently, zooplankton biomass responded positively to enrichment with light over the entire mixing depth gradient.

Mixed surface layer depth is determined by climatic conditions, lake size and orientation, and water clarity (Sterner 1990; Fee et al. 1996). Not surprisingly, global warming has already been related to changes in stratification patterns (e.g., earlier onset and delayed breakdown of stratification in central European lakes, extended duration of spring turnover in Scandinavian lakes, and increased summer stratification depth of small Canadian lakes; Fee et al. 1996; Weyhenmeyer et al. 1999; Livingstone 2003). On the basis of our zooplankton data, we furthermore expect that the effects of mixing depth predicted by our model should propagate to higher trophic levels. We therefore suggest that a better understanding of the consequences of global climate change for carbon and nutrient dynamics of pelagic food chains will require improved knowledge about the effects of climate on stratification patterns.

References

Andersen, T. 1997. Pelagic nutrient cycles: herbivores as sources and sinks. Springer-Verlag.

———, J. J. Elser, and D. O. Hessen. 2004. Stoichiometry and population dynamics. Ecol. Lett. **7:** 884–900.

Botrell, H. H., and others. 1976. A review of some problems in zooplankton production studies. Nor. J. Zool. **24:** 419–456.

Boyd, P. W. 2002. Environmental factors controlling phytoplankton processes in the Southern Ocean. J. Phycol. **38:** 844–861.

Cebrian, J. 1999. Patterns in the fate of production in plant communities. Am. Nat. **154:** 449–468.

Diehl, S. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: Theory. Ecology **83:** 386–398.

———, S. A. Berger, R. Ptacnik, and A. Wild. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: Field experiments. Ecology **83:** 399–411.

———, ———, and R. Wöhrl. 2005. Flexible algal nutrient stoichiometry mediates environmental influences on phytoplankton and its abiotic resources. Ecology **86:** 2931–2945.

Droop, M. R. 1974. Nutrient status of algal cells in continuous culture. J. Mar. Biol. Assoc. UK **54:** 825–855.

Fee, E. J., R. E. Hecky, S. E. M. Kasian, and D. R. Cruikshank. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnol. Oceanogr. **41:** 912–920.

Guildford, S. J., L. L. Hendzel, H. J. Kling, E. J. Fee, G. G. C. Robinson, R. E. Hecky, and S. E. M. Kasian. 1994. Effects of lake size on phytoplankton nutrients status. Aquat. Sci. **51:** 2769–2783.

Hansson, L. A., and others. 1998. Consumption patterns, complexity and enrichment in aquatic food chains. Proc. R. Soc. Lond., B **265:** 901–906.

Hessen, D. O. 1992. Nutrient element limitation of zooplankton production. Am. Nat. **140:** 799–814.

———, G. I. Agren, T. R. Anderson, J. J. Elser, and P. C. De Ruiter. 2004. Carbon, sequestration in ecosystems: The role of stoichiometry. Ecology **85:** 1179–1192.

Huisman, J. 1999. Population dynamics of light-limited phytoplankton: Microcosm experiments. Ecology **80:** 202–210.

———, AND F. J. WEISSING. 1994. Light-limited growth and competition for light in well-mixed aquatic environments—an elementary model. Ecology **75:** 507–520.

———, AND ———. 1995. Competition for nutrients and light in a mixed water column: A theoretical analysis. Am. Nat. **146:** 536–564.

KUNZ, T. J., AND S. DIEHL. 2003. Phytoplankton, light and nutrients along a gradient of mixing depth: A field test of producer-resource theory. Freshw. Biol. **48:** 1050–1063.

LIVINGSTONE, D. M. 2003. Impact of secular climate change on the thermal structure of a large temperate central European lake. Clim. Chang. **57:** 205–225.

MCCAULEY, E., AND J. KALFF. 1981. Empirical relationships between phytoplankton and zooplankton biomass. Can. J. Fish. Aquat. Sci. **38:** 458–463.

MITCHELL, B. G., AND O. HOLM-HANSEN. 1991. Observations and modelling of the Antarctic phytoplankton crop in relation to mixing depth. Deep-Sea Res. Oceanogr., A **38:** 981–1007.

MOREL, F. M. M. 1987. Kinetics of nutrient-uptake and growth in phytoplankton. J. Phycol. **23:** 137–150.

MULLER, E. B., R. M. NISBET, S. A. L. M. KOOIJMAN, J. J. ELSER, AND E. MCCAULEY. 2001. Stoichiometric food quality and herbivore dynamics. Ecol. Lett. **4:** 519–529.

MURDOCH, W. W., R. M. NISBET, E. MCCAULEY, A. M. DEROOS, AND W. S. C. GURNEY. 1998. Plankton abundance and dynamics across nutrient levels: Tests of hypotheses. Ecology **79:** 1339–1356.

PERSSON, L., S. DIEHL, L. JOHANSSON, G. ANDERSSON, AND S. F. HAMRIN. 1992. Trophic interactions in temperate lake ecosystems—a test of food-chain theory. Am. Nat. **140:** 59–84.

PETERS, R. H. 1986. The role of prediction in limnology. Limnol. Oceanogr. **31:** 1143–1159.

PTACNIK, R., S. DIEHL, AND S. A. BERGER. 2003. Performance of sinking and non-sinking phytoplankton taxa in a gradient of mixing depths. Limnol. Oceanogr. **48:** 1903–1912.

RASTETTER, E. B., G. I. AGREN, AND G. R. SHAVER. 1997. Responses of N-limited ecosystems to increased CO_2: A balanced-nutrition, coupled-element-cycles model. Ecol. Appl. **7:** 444–460.

SENFT, H. 1978. Dependence of light-saturated rates of algal photosynthesis on intracellular concentrations of phosphorus. Limnol. Oceanogr. **23:** 709–718.

SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. **106:** 433–471.

SOTO, D. 2002. Oligotrophic patterns in southern Chilean lakes: The relevance of nutrients and mixing depth. Rev. Chil. Hist. Nat. **75:** 377–393.

STERNER, R. W. 1990. Lake morphometry and light in the surface-layer. Can. J. Fish. Aquat. Sci. **47:** 687–692.

———. 1997. Modelling interactions of food quality and quantity in homeostatic consumers. Freshw. Biol. **38:** 473–481.

———, J. CLASEN, W. LAMPERT, AND T. WEISSE. 1998. Carbon : phosphorus stoichiometry and food chain production. Ecol. Lett. **1:** 146–150.

———, J. J. ELSER, E. J. FEE, S. J. GUILDFORD, AND T. H. CHRZANOWSKI. 1997. The light : nutrient ratio in lakes: The balance of energy and materials affects ecosystem structure and process. Am. Nat. **150:** 663–684.

URABE, J., M. KYLE, W. MAKINO, T. YOSHIDA, T. ANDERSEN, AND J. J. ELSER. 2002. Reduced light increases herbivore production due to stoichiometric effects of light/nutrient balance. Ecology **83:** 619–627.

———, AND R. W. STERNER. 1996. Regulation of herbivore growth by the balance of light and nutrients. Proc. Natl. Acad. Sci. USA **93:** 8465–8469.

———, AND J. WATANABE. 1992. Possibility of N or P limitation for planktonic cladocerans: An experimental test. Limnol. Oceanogr. **37:** 244–251.

VISSER, P. M., L. MASSAUT, J. HUISMAN, AND L. R. MUR. 1996. Sedimentation losses of *Scenedesmus* in relation to mixing depth. Arch. Hydrobiol. **136:** 289–308.

VOLLENWEIDER, R. A. 1976. Advances in defining the critical loading levels for phosphorus in lake eutrophication. Mem. Ist. Ital. Idrobiol. **33:** 53–83.

WEYHENMEYER, G. A., T. BLENCKNER, AND K. PETTERSSON. 1999. Changes of the plankton spring outburst related to the North Atlantic oscillation. Limnol. Oceanogr. **44:** 1788–1792.

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