

Environmental and algal forcing of *Daphnia* production dynamics

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Abstract

Recent studies of lakes suggest that the relative availability of light and phosphorus in the mixed layer helps determine the quality of phytoplankton consumed by herbivorous zooplankton. In turn, increases in algal quality positively affect zooplankton growth and reproductive rates. However, these studies have concentrated on explaining variation among lakes over relatively short time periods and have not evaluated the temporal dynamics in the physical–chemical forcing on zooplankton production. We investigated whether there were seasonal changes in the relationship between *Daphnia* fecundity and the physical–chemical environment, algal community characteristics, and *Daphnia* length using dynamic linear models (DLM) to analyze a high-resolution, 16-yr time series from Lake Washington. We used two metrics to describe algal quality: the percentage of blue-green algae and the light to total phosphorus (TP) ratio as an indirect metric for algal C:P. Chlorophyll *a* (Chl *a*) concentration and algal biovolume served as measures of algal quantity. As expected, both the light:TP ratio and the percentage of blue-green algae had negative effects on *Daphnia* fecundity, and Chl *a* concentration and biovolume had positive effects on fecundity. However, we found a comparatively stronger effect of *Daphnia* length on fecundity, although it was negative and therefore opposite to expectation. In all cases, we observed strong seasonal differences in environmental effects, but no temporal change in the fundamental relationships between our indices of algal quantity and quality, allometry, and *Daphnia* reproduction. Our results support a hypothesis of physical–chemical coupling to algal quality and zooplankton production but highlight the importance of temporal variation in this forcing.

Much of the current emphasis in food web studies attempts to predict the degree to which food web structure controls primary producers and the efficiency with which primary production is transferred to upper trophic levels (e.g., Carpenter and Kitchell 1993; Polis and Winemiller 1994). In aquatic ecosystems, zooplankton can exert strong control over phytoplankton. These grazers affect their phytoplankton food directly through grazing (Sommer et al. 1986) or indirectly through nutrient recycling (Lehman 1980). In turn, the nutritional quality of primary producers can control the composition of the herbivore community and rates of secondary production (Gulati and Demott 1997). In addition to algal quality, algal quantity might also limit zooplankton production (Lynch 1989). Furthermore, the body size of an individual can also affect its fecundity (Lampert 1993); therefore, the size structure of the zooplankton community might play an important role in overall secondary production rates in aquatic ecosystems. However, there have been no formal quantitative analyses of the relative importance of each of these factors in governing secondary production rates in zooplankton.

The emergence of ecological stoichiometry has led to a greater understanding of the relationship between grazers, their food source, and the abiotic environment (Elser and

Urabe 1999). Because the C:N:P ratios vary among different zooplankton taxa, the relative rates at which zooplankton acquire and recycle these nutrients have important implications for zooplankton growth rates (Main et al. 1997) and phytoplankton dynamics (Sarnelle 1992). When consuming low-quality food, zooplankton growth can be constrained by their ability to synthesize and maintain vital biochemical cell constituents (Elser et al. 1996). In particular, *Daphnia* have high requirements for P and are therefore susceptible to P nutritional constraints on growth (Urabe et al. 1997). The C:P ratio is one representation of the “quality” of the phytoplankton as a food source for zooplankton. Other aspects of food quality include algal fatty acid content (Müller-Navarra et al. 2000) and phytoplankton community composition (Demott 1999).

Predicting the effects of environmental conditions on the relative importance of algal quality versus algal quantity on zooplankton production remains an important goal in aquatic ecology (Brett et al. 2000). Variation in the ratio of light exposure to nutrient supply has been suggested as a principle driver of the carbon to phosphorus ratio (C:P) (Sterner et al. 1997). At a fixed level of phosphorus, increased light leads to increased C fixation and thereby decreases the relative amount of P in the algae, resulting in a decrease in algal quality. However, the mechanism and extent to which the abiotic environment controls algal quality in lakes remain poorly understood. Much of our understanding to date has relied on lab experiments (e.g., Elser et al. 2001) or comparative studies of different ecosystems (e.g., Dobberfuhl and Elser 2000). Strong intra- and interannual variation in the physical, chemical, and biological properties of lakes may produce an environment with large differences in the interaction among trophic levels. However, there has been essentially no exploration of the temporal organization of environmental forcing on algal quality and subsequent patterns of secondary production in lakes.

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Acknowledgments

M.D.S. and D.E.S. gratefully acknowledge the foresight of W. T. Edmondson in realizing the benefit of maintaining a long-term database on Lake Washington. Sally Abella and Jennifer Anson helped with database management. Mike Brett and Peter Leavitt provided useful comments during the course of this study. Support from the Andrew W. Mellon Foundation funded much of the data collection. The Andrew W. Mellon Foundation and an NSF graduate training grant in mathematical biology supported M.D.S.

The plankton of Lake Washington have been studied intensively since 1949 (Edmondson 1994). The time series data derived from these studies allowed us to investigate how seasonal changes in the physical and chemical environment are transmitted to zooplankton production dynamics via temporal changes in surrogates of algal quality and quantity in Lake Washington. Specifically, we measured the relative strengths of algal quality, algal quantity, and *Daphnia* length as predictors of *Daphnia* fecundity. Our results support the contention that the physical–chemical environment controls zooplankton production through its effect on food quality while emphasizing the importance of temporal organization in the coupling between phytoplankton and zooplankton production.

Methods

We used the chlorophyll *a* (Chl *a*) concentration and total algal biovolume as metrics for algal quantity (Felip and Catalan 2000) and the proportion of blue-green algae and the light:total phosphorus (TP) ratio as surrogates for algal quality. We based the latter assumption on the findings of Sterner et al. (1997), who found a strong positive relationship between light:TP and algal C:P ($r^2 = 0.85$). Rather than first predict algal C:P from light:TP and then calculate the effect of C:P on *Daphnia* fecundity, we used light:TP as a predictor of *Daphnia* fecundity to avoid compounding the errors from the first regression. Furthermore, our goal was to explore whether simple measures of the physical and chemical environment, such as light and TP, have any ability to predict *Daphnia* fecundity. Therefore, we adopt the convention of using algal quality to refer to the effects of blue-green algae and light:TP, and algal quantity to refer to the effect of Chl *a* concentration and algal biovolume.

Limnological data—Lake Washington is a large (87.6 km²), mesotrophic lake located within the city of Seattle, Washington. Standard limnological data from Lake Washington, including zooplankton abundance, Chl *a* concentration, algal biovolume and community composition, total phosphorus, thermal profile, and Secchi depth, were collected over weekly to monthly intervals from 1977 to 1992. We concentrated on this time period because *Daphnia* were rare in the lake before 1975 and then found only sporadically until 1977 (Edmondson 1994). Lake water was collected from 0 to 10 m using an integrated-depth tube sampler. Following persulfate digestion and subsequent reaction with molybdate and stannous chloride, total phosphorus (TP) concentration was determined colorometrically by reading the samples on a spectrophotometer at 720 nm and comparing them to a standard curve (Anonymous 1999). Chl *a* concentration was determined by filtering lake water through 0.7- μ m membrane filters, grinding the filters, and dissolving them in acetone. Following centrifuging, the samples were read on a spectrophotometer at 663 nm, corrected for phaeopigments, and compared to a standard curve (Strickland and Parsons 1972). We estimated algal biovolume using simple geometric analogs. At least 50 cells or colonies were measured to characterize the size range in the population, and

then individual size was multiplied by density to obtain total biovolume.

Zooplankton were collected from 0 to 20 m with a Clark–Bumpus sampler fitted with a 130- μ m net and a flowmeter to calculate the total sample volume (Edmondson and Litt 1982). We combined all *Daphnia* species (*D. pulicaria*, *D. thorata*, *D. galeata mendotae*) and based their sexual maturity on the relative size of the first two processes on the postabdominal claw (Edmondson and Litt 1982). Mean fecundity was calculated as the mean number of eggs per adult female. *D. pulicaria* averaged 70% of the *Daphnia* biomass across all samples and should therefore help to minimize species composition effects. Finally, we averaged all of these data over monthly intervals in an attempt to maximize within-year samples and minimize the number of missing values. This produced a time series of 192 observations. To determine *Daphnia* mean length, we measured at least 50 *Daphnia* to the nearest 0.01 mm and averaged them over monthly intervals. However, we were only able to reconstruct a shorter time series of *Daphnia* length data from 1985 to 1992 ($n = 65 = 94 - 29$ missing data points). Therefore, from here on we will refer to the two time series as “long” and “short,” respectively.

Following the notation of Sterner et al. (1997), we calculated the mean light in the mixed layer (I_m , dimensionless) as a fraction of the surface light using the formula

$$I_m = \frac{1 - e^{-Kz_m}}{Kz_m} \quad (1)$$

where the extinction coefficient (K , m⁻¹) is calculated from the Secchi depth (z_{sd} , m) using the relationship $K = 1.54/z_{sd}$. We calculated the depth of mixing (z_m , m) as the maximum depth where the water temperature varies $\leq 1^\circ\text{C}$ relative to the temperature at 0.5 m.

Time series analyses—We used Dynamic Linear Models (DLM) fit to times series data (Pole et al. 1994) as a tool for evaluating the ability of food quality, food quantity, and allometric hypotheses in predicting *Daphnia* fecundity dynamics. We also added an environmental effect to the model to allow for additional seasonal effects on *Daphnia* fecundity dynamics. This environmental effect represents an aggregate of exogenous variables that we have not accounted for explicitly (e.g., actual light intensity, water temperature, specific algal species composition) but that allows us to evaluate the seasonal variation in *Daphnia* fecundity dynamics. This technique has been applied effectively to ecological data, and the methodology has been described in detail elsewhere (e.g., Cottingham and Carpenter 1998; Lamon et al. 1998), so we will only describe it briefly here.

Our model formulation begins with the familiar general linear model

$$\mathbf{Y} = \mathbf{X}\theta + \nu \quad (2)$$

where an $n \times 1$ vector of response variables (\mathbf{Y}) are set equal to an $n \times m$ matrix of predictor variables (\mathbf{X}) times an $m \times 1$ vector of regression parameters, plus an $n \times 1$ vector of observation errors (ν). In our case, the vector \mathbf{Y} would represent the observed eggs per female *Daphnia* and the different forms of matrix \mathbf{X} would represent the various

competing models. For our first analysis of the long time series, \mathbf{X} contained all one- and two-variable combinations of the following four variables: Chl *a* concentration, algal biovolume, the light:TP ratio, and the proportion of blue-green algae (total of 10 combinations). For the second analysis of the short time series, \mathbf{X} contained each of the previous four variables alone, plus *Daphnia* mean length alone, plus each of the original four variables combined with *Daphnia* length (total of nine combinations).

For the dynamic form of the model, we express the relationship in a similar fashion but introduce an explicit time-ordered index to the vectors and matrices. In this case, at each time step t the observed response variable (Y_t , a scalar) is sequentially fitted to the $1 \times m$ vector of predictor variables (\mathbf{X}_t) with the $m \times 1$ regression parameter vector (θ_t) plus an error term (ν_t , a scalar) according to the observation equation

$$Y_t = \mathbf{X}_t \theta_t + \nu_t \quad \nu_t \sim N[0, V_t] \quad (3)$$

This model formulation has two features that distinguish it from the time-invariant model (Eq. 2). First, the observed data are explicitly time ordered (i.e., Y_1, Y_2, \dots, Y_t) and second, the regression parameters are allowed to vary through time. The observation errors ν_t have a variance V_t that is time-dependent and is usually not known well enough to approximate it with a fixed value. Therefore, as the analysis proceeds through time, V_t is estimated from all of the prior data by assuming it is equal to the inverse of the precision ($V_t = \phi_t^{-1}$). Following Pole et al. (1994), we assume that ϕ_t is gamma distributed as

$$\phi_t \sim G[n_{t-1}/2, d_{t-1}/2] \quad (4)$$

such that n_{t-1} is the degrees of freedom and d_{t-1} is the sum of squared errors. The discounting scheme described below also applies to V_t .

The parameter set in the general linear model (Eq. 2) is the same for all observations (i.e., every observation contains information on each parameter). However, the DLM makes use of changes in the parameter set over time through a system equation. Using prior information from Bayesian learning, the $m \times 1$ vector of regression parameters (θ_t) evolves through time according to the first-order Markov process

$$\theta_t = \mathbf{G} \theta_{t-1} + \omega_t \quad \omega_t \sim N[\mathbf{0}, \mathbf{W}_t] \quad (5)$$

The $m \times m$ system evolution matrix \mathbf{G} dictates how the parameters change systematically through time while the $m \times 1$ variance vector ω_t describes the stochastic change in each of the parameter estimates (θ_t) over time. The system variance matrix (\mathbf{W}_t) has the variance in ω_t along the diagonal and zeros elsewhere. It is determined by the component discount factors applied to the previous time step's posterior covariance matrix (Pole et al. 1994).

One-step forecasts are generated at each time step and the parameters are updated as new information becomes incorporated into the model. Through the use of discounting, priors are given weights that determine how influential the prior data are when updating the parameter estimates. These discounts represent the rate of exponential decay of useful information such that when the discount is 1 (its maximum

value), all of the prior information is retained, whereas a discount of 0 means no prior information is used at all. In general, the lower the discount value, the faster a parameter can change through time. For example in our case, setting the discount to 0.9 would use the last 26 data points. We selected the discounts by varying them systematically and then minimizing the negative log-likelihood of the overall model.

As an example, consider the case where we want to predict the effect of Chl *a* concentration on *Daphnia* fecundity, while including the seasonal effect of month, and assuming a constant trend (i.e., an underlying intercept or "level," but no increase or decrease in the series over time). At $t = 1$, the parameter (θ_t) and predictor vectors (\mathbf{X}_t) would be generated from the level (α), predictor (β), and seasonal ($\mu_{\text{month},t}$) effects, respectively, to give

$$\theta_t = (\alpha_1 \beta_1 \mu_{1,1} \mu_{2,1} \mu_{3,1} \mu_{4,1} \mu_{5,1} \mu_{6,1} \mu_{7,1} \mu_{8,1} \mu_{9,1} \mu_{10,1} \mu_{11,1} \mu_{12,1})' \quad \text{and} \quad (6)$$

$$\mathbf{X}_t = (1 [\text{Chl } a]_t 1 0 0 0 0 0 0 0 0 0 0) \quad (7)$$

The evolution matrix (\mathbf{G}) would have the following form.

$$\mathbf{G} = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (8)$$

The dotted lines within \mathbf{G} delineate the three square submatrices along the diagonal representing the transition rules for the level ($n = 1$), regression predictor ($n = 1$), and seasonal ($n = 12$) parameters, respectively. At each permutation of (Eq. 3), the evolution matrix \mathbf{G} causes the 12 seasonal parameters within θ_t to shift such that only one monthly parameter corresponding to the current month is included when multiplied by \mathbf{X}_t in (Eq. 2). Pole et al. (1994) offer a more detailed discussion of the general model development, and Lamon et al. (1998) provide a comprehensive example of the methodology applied to ecological data.

We began by comparing each competing model to (1) a reference model containing an underlying level plus a seasonal effect, but no regression effect, and (2) the same model minus a specific seasonal component. Finally, we compared each of the models minus their seasonal component to the reference model. For the first two comparisons, we assessed model performance through the use of a likelihood ratio test, which is appropriate for testing nested models (Hilborn and Mangel 1997). To compare any full model A with a reference model B, the test statistic (R) was computed as twice the difference in negative log-likelihood, $L(x|\cdot)$, according to

$$R = 2[L(x|B) - L(x|A)] \quad R \sim \chi^2(\text{df}) \quad (9)$$

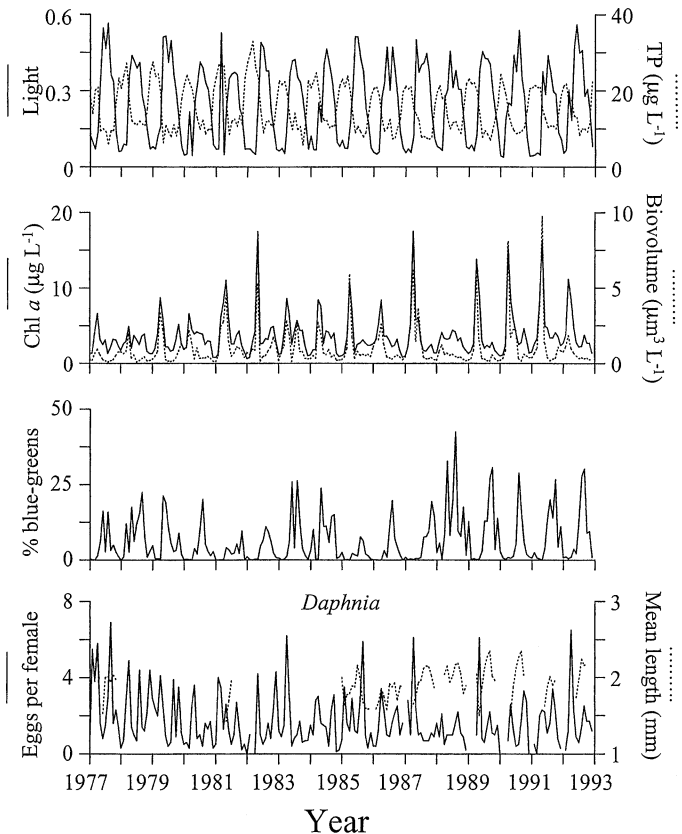


Fig. 1. Lake Washington time series data from 1977 to 1992 for the amount of light in the mixed layer (Light), total phosphorus (TP), chlorophyll *a* concentration (Chl *a*), algal biovolume (Biovolume), percent blue-green algae by biovolume (% Blue-greens), *Daphnia* fecundity, and *Daphnia* mean length. Note that *Daphnia* length data only exist for parts of 1977, 1982, and 1985–1992. The variable Light is a dimensionless fraction of the surface light; see *Methods* for a description of the formula used.

The degrees of freedom (df) for the test equal the difference in the number of parameters between models A and B. The same comparison was then made for a full model A with its comparable nonseasonal model C. We then ranked the competing predictive models in order of increasing performance according to the Bayes Information Criterion (BIC), where

$$\text{BIC} = 2L(x|\cdot) + p \log_e(n) \quad (10)$$

L is the negative log-likelihood, p equals the number of parameters in the model, and n is the sample size (Box et al. 1991).

For pairwise comparisons between any two models i and j ($i < j$), we used the Schwarz criterion (Kass and Raftery 1995)

$$S_{ij} = (\text{BIC}_j - \text{BIC}_i)/2 \quad (11)$$

The Schwarz criterion is an approximation to a true Bayes Factor (B_{ij}):

$$S_{ij} \cong \log_e(B_{ij}) \quad (12)$$

According to Kass and Raftery (1995), when $2S_{ij} = 2 \log_e(B_{ij})$ is 0–2, the evidence favoring the higher ranked

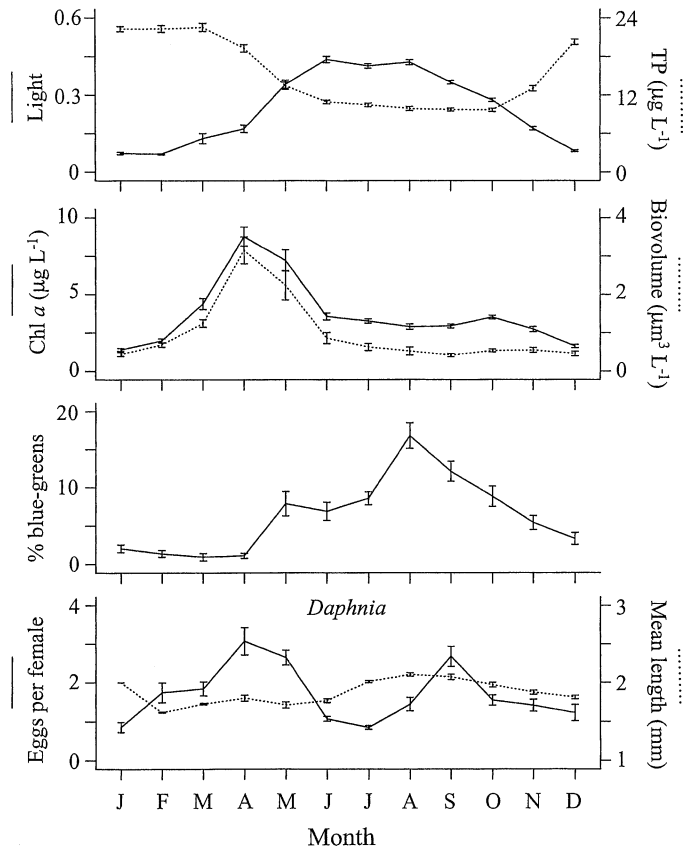


Fig. 2. Monthly means of the Lake Washington time series data (1977–1992) described in Fig. 1. Error bars represent 95% confidence intervals ($n = 16$ per month). Mean *Daphnia* length is based on partial years of data from 1977, 1982, and 1985–1992, with $n = 1$ –8.

model is “not worth more than a bare mention”; a value of 2–6 indicates “positive” and 6–10 and <10 offers “strong” and “very strong” evidence, respectively, for model i over model j (see *Tables 3, 5*). The Schwarz criterion also allowed us to compare all nonseasonal models with a model including only seasonal effects.

Results

The time series data from Lake Washington demonstrated considerable inter- and intra-annual variation (Fig. 1), but closer examination of the monthly mean values revealed consistent intra-annual trends (Fig. 2). Light and TP were negatively correlated, with the peak in light occurring in May–June and the peak in TP occurring in January–March. Chl *a* concentration and algal biovolume both reached their maximum values in April and May, although they also were most variable during these months, largely as a function of the timing of spring stratification. Blue-green algae constituted a small percentage of the phytoplankton community throughout the winter and spring before rising in May and then peaking in August. *Daphnia* fecundity was bimodal, with consistent peaks in April and September, whereas *Daphnia* mean length remained relatively constant across

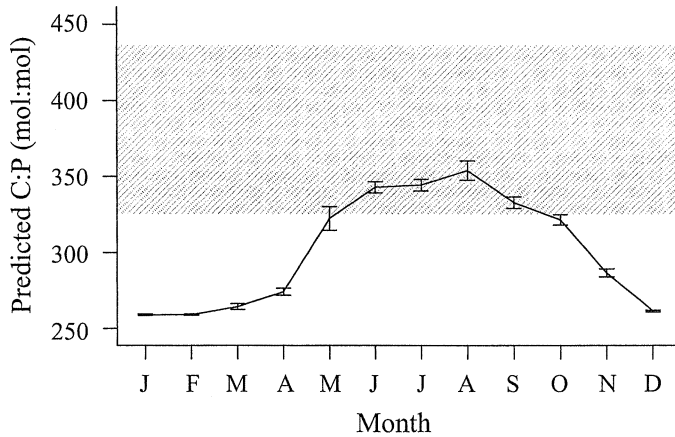


Fig. 3. Monthly means ($\pm 95\%$ CI) of the C:P ratio predicted from light:TP based on the relationship of Sterner et al. (1997) ($C:P = 252 + 71 \cdot \text{light:TP}$, $r^2 = 0.85$). The shaded region of the graph indicates the lower range of C:P ratios where algal food quality is thought to be a limiting factor in *Daphnia* production (Hessen 1992).

months with a slight increase during late summer. Although we do not have direct estimates of algal C:P ratios, we made predictions about the likely range of their values in Lake Washington based on the relationship of Sterner et al. (1997). We found that the predicted algal C:P ratio in Lake Washington varied between 250 and 350 and rose into the region where it constrains zooplankton production in May–October (Fig. 3).

Simple linear regressions using the metrics of food quantity, food quality, and *Daphnia* length to predict *Daphnia* fecundity demonstrated mixed results (Table 1). We found a weak, but significantly positive, relationship between algal quantity (both Chl *a* and biovolume) and fecundity. We observed no significant relationship between algal quality (percent blue-green algae and the surrogate, light:TP) and *Daphnia* fecundity. Finally, we found a marginally signifi-

Table 1. Comparison of regression performance to predict *Daphnia* fecundity for a simple linear regression model and the seasonal DLM based upon the r^2 and P -value of the full regression model. The predictor variables are chlorophyll *a* concentration (Chl *a*), algal biovolume (BV), the light:TP ratio (L:TP), proportion of blue-green algae (BG), and *Daphnia* mean length (length).

Predictor	Simple linear		DLM	
	r^2	P	r^2	P
Chl <i>a</i>	0.12	<0.001	0.36	0.002
BV	0.032	0.016	0.33	0.006
BG	0.010	0.17	0.34	<0.001
L:TP	0.0013	0.63	0.35	<0.001
Length	0.042	0.080	0.70	<0.001

cant negative relationship between *Daphnia* length and fecundity. However, these results are conservative estimates of the relationships because simple linear regression assumes that each of the data points is independent. This is not the case here where the time series data are temporally autocorrelated and the time ordering of the data may represent a substantial source of information about the relationships between variables. Using the DLM approach, which explicitly accounts for the temporal organization of the time series, we found a significant relationship between all of the predictor variables and *Daphnia* fecundity, and greatly improved the predictive capability of the models (Table 1).

The DLM method indicated that food quality models (light:TP and percent blue-green algae) fit the observed data best (Table 2). The next three highest ranked models all included Chl *a* (i.e., food quantity) as a predictor (Table 2). According to the Schwarz criterion, the light:TP model had essentially no evidence favoring it over the percent blue-green algae model (Table 3), but both of the food quality models had very strong evidence favoring them over any of the food quantity or mixed models (Table 3). The effects of algal quality and quantity on *Daphnia* fecundity, measured as the product of the predictor variable and its regression

Table 2. DLM results for the analysis of the long time series (1977–1992, $n = 192$) using models that explicitly account for monthly seasonal effects. Models are ranked in terms of overall performance in predicting *Daphnia* fecundity. Rank is assigned in order of increasing BIC. The “Ref” model represents a simple random walk. Class refers to the type of predictor variable(s) in terms of algal food constraints on *Daphnia* fecundity. The predictor variables are described in Table 1, with the sign of the regression coefficient for each predictor variable in parentheses following it. See the Methods section for a description of BIC calculations. The likelihood ratio (λ) P -values indicate whether any given model performs significantly better than the reference model and its comparable nonseasonal model.

Rank	Class	Predictors		Parameters	BIC	λ P -values	
		X_1	X_2			Reference	Nonseason
Ref				13	178.3	—	<0.001
1	Quality	L:TP(-)		14	154.8	<0.001	<0.001
2	Quality	BG(-)		14	156.3	<0.001	<0.001
3	Mixed	Chl <i>a</i> (+)	BV(-)	15	166.8	<0.001	<0.001
4	Quantity	Chl <i>a</i> (+)		14	173.8	0.002	<0.001
5	Mixed	L:TP(-)	Chl <i>a</i> (+)	15	174.1	0.001	<0.001
6	Mixed	BG(-)	Chl <i>a</i> (+)	15	175.3	0.001	<0.001
7	Mixed	BV(+)	L:TP(-)	15	175.3	0.001	<0.001
8	Quantity	BV(+)		14	176.0	0.006	<0.001
9	Mixed	BV(+)	BG(-)	15	176.9	0.003	<0.001
10	Mixed	L:TP(-)	BG(-)	15	177.6	0.004	<0.001

Table 3. Pairwise comparisons of DLM model performance for the long time series based on twice the Schwarz criterion (2S). Model numbers refer to those in Table 2. See Methods for statistical description and equations. Any model at the top of a column can be compared to any lower ranked model in subsequent rows (e.g., Model 1 vs. 5 = 19, 3 vs. 4 = 7.0). According to Kass and Raftery (1995), a number from 0 to 2 means the evidence favoring the higher ranked model is “not worth more than a bare mention”; 2–6 indicates “positive,” 6–10 offers “strong,” and >10 provides “very strong” evidence.

Model	Model								
	1	2	3	4	5	6	7	8	9
2	1.5								
3	12	10							
4	19	17	7.0						
5	19	18	7.3	0.33					
6	20	19	8.5	1.6	1.2				
7	21	19	8.5	1.6	1.2	0.0082			
8	21	20	9.2	2.2	1.9	0.69	0.68		
9	22	21	10	3.2	2.8	1.6	1.6	0.93	
10	23	21	11	3.8	3.5	2.2	2.2	1.5	0.62

coefficient ($\mathbf{X}_i\theta_i$), matched our predictions. The distribution of effect sizes from the DLMS indicated a negative effect of the food quality metrics on *Daphnia* fecundity, as illustrated by light:TP and the amount of blue-green algae (Fig. 4). Conversely, food quantity as represented by Chl *a* had a positive effect on *Daphnia* fecundity. However, biovolume actually had a negative effect when it was added as a second predictor with Chl *a* (Fig. 4).

Analyses of the short time series indicated a strong relationship between *Daphnia* length and fecundity (Table 4). Indeed, the top five models all included length as a predictor variable and had very strong evidence favoring them over any nonlength model (Table 5). Based on BIC, the mixed model of length plus Chl *a* performed best. However, the Schwarz criterion provided very little evidence to support it over the second-ranked length-only model (Table 5). Although *Daphnia* length provided the best fit to the observed fecundity, its effect on fecundity was strongly negative and therefore the opposite of what we expected (Fig. 5).

Finally, we found no significant difference in any of the

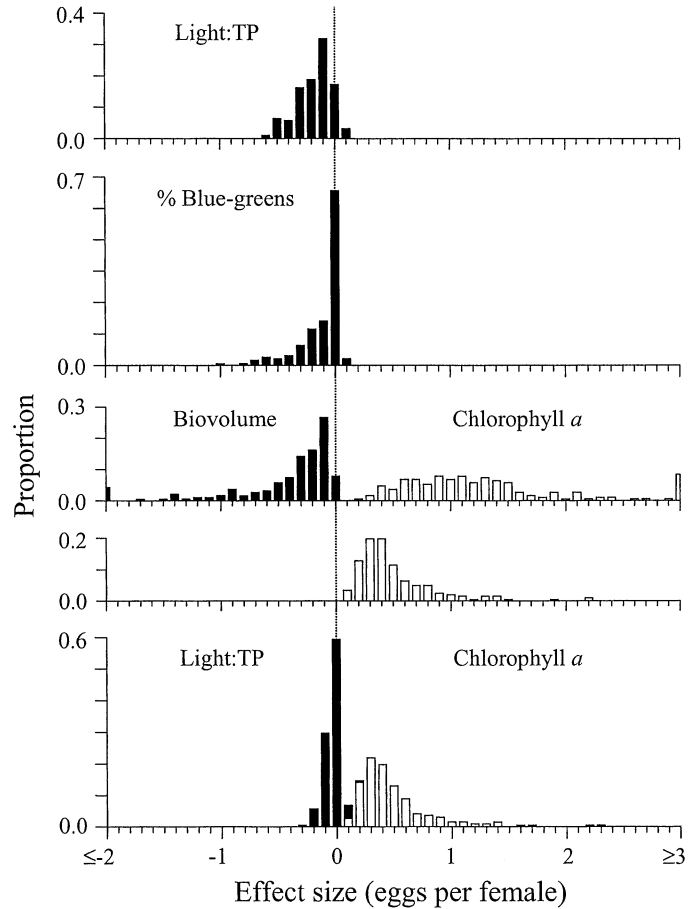


Fig. 4. Distribution of DLM effect sizes for the five highest ranked models listed in Table 1.

main effects across months (ANOVA, $F_{1,11} < 0.5$, $P > 0.9$ for all comparisons). However, the aggregate seasonal effect varied significantly across months (ANOVA, $F_{1,11} > 230$, $P < 0.0001$ for all comparisons). A negative exponentially weighted least squares fit through the seasonal data from the top five long series models plus the length-only model from the short time series indicated a positive effect of the aggregate environmental variable in late spring (April–May) and

Table 4. DLM results for the analysis of the short time series (1985–1992, $n = 65$) to include the effect of *Daphnia* length, using models that explicitly account for monthly seasonal effects. Descriptions of the table columns are the same as those in Tables 1 and 2.

Rank	Class	Predictors		Parameters	BIC	P-values	
		X_1	X_2			Reference	Nonseason
Ref				13	93.3	—	0.017
1	Mixed	Length(–)	Chl <i>a</i> (+)	15	73.2	<0.001	0.060
2	Allometric	Length(–)		14	73.2	<0.001	0.016
3	Mixed	Length(–)	BV(+)	15	75.4	<0.001	0.020
4	Mixed	Length(–)	BG(–)	15	75.8	<0.001	0.019
5	Mixed	Length(–)	L:TP(–)	15	76.2	<0.001	0.019
6	Quantity	Chl <i>a</i> (+)		14	83.6	<0.001	0.038
7	Quality	BG(–)		14	91.8	0.018	0.014
8	Quantity	BV(+)		14	92.4	0.025	0.014
9	Quality	L:TP(–)		14	92.6	0.028	0.009

Table 5. Pairwise comparisons of DLM model performance for the short time series based on twice the Schwarz criterion (2S). Model numbers refer to those in Table 3. Column and row descriptions are the same as Table 3.

Model	Model								
	1	2	3	4	5	6	7	8	
2	0.026								
3	2.2	2.2							
4	2.6	2.6	0.40						
5	3.0	3.0	0.80	0.40					
6	10	10	8.2	7.8	7.4				
7	19	19	16	16	16	8.2			
8	19	19	17	17	16	8.8	0.60		
9	19	19	17	17	16	9.0	0.80	0.20	

again in September (Fig. 6). The aggregate environmental variable had the greatest negative effect in midsummer (June and July) and a slight negative effect in late fall and early winter (November–January). In all cases, the models that included a seasonal effect were better predictors than their nonseasonal counterparts (Tables 3, 5). However, all but one of the nonseasonal models provided “very strong” evidence favoring them over the season-only reference model (Table 6). This suggests that ecological structure by itself is still more important than just accounting for seasonal effects.

Discussion

Physical and chemical conditions have been proposed to control the efficiency of nutrient use at the base of lake food webs (Sterner et al. 1997). In particular, when light energy in the mixed layer is high relative to phosphorus availability, algae are carbon-rich and nutrient-deficient, leading to poor algal quality as food for zooplankton grazers (Urabe and Sterner 1996; Sterner et al. 1998). Furthermore, several studies have shown the important effect of algal quality on zooplankton production (Sterner and Hessen 1994; Elser et al. 1998; Müller-Navarra et al. 2000). As the elemental stoichiometry of zooplankton taxa varies, so does their relative requirement for C, N, and P. Relative to copepods, the *Daphnia* N:P ratio is generally lower because of their relatively high requirement of P for cell constituents such as phospholipids, ATP/ADP, and nucleic acids (Elser et al. 1996). Subsequently, when their food sources are relatively high in P,

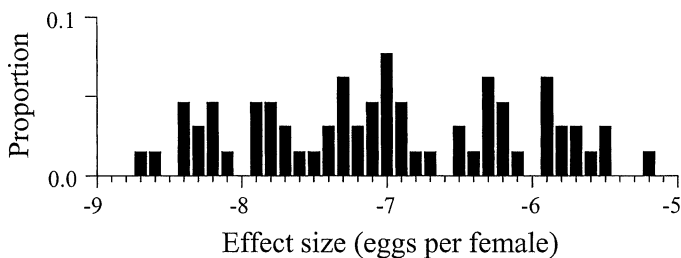


Fig. 5. Distribution of DLM effect size with only *Daphnia* length as a predictor of *Daphnia* fecundity (model 2) based on the DLM for the short time series (1985–1992).

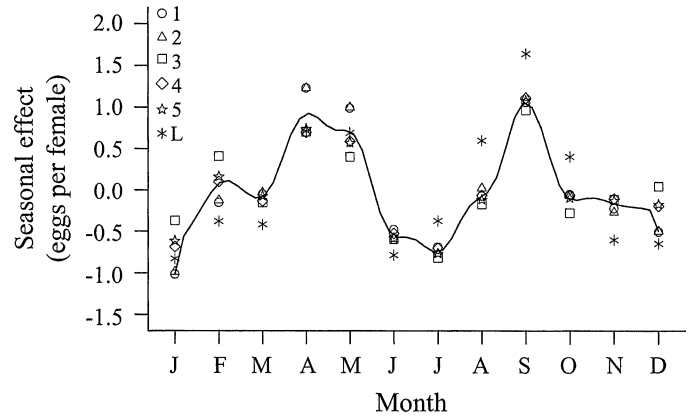


Fig. 6. Seasonal effects of environmental forcing from the DLM analyses of the five models shown in Fig. 4 (numbers 1–5) plus the seasonal effect from the length-only model shown in Fig. 5 (L). The line represents a best-fit curve based on a negative exponential weighting function.

Daphnia exhibit increased growth rates because of greater requirements for P-rich ribosomal RNA (Main et al. 1997).

Combining the above models for the effect of light:TP on algal quality and the subsequent effect of algal quality on *Daphnia* production, we expected a negative relationship between light:TP and *Daphnia* fecundity (sensu Sterner et al. 1997). Indeed, we found a strong negative relationship between light:TP and *Daphnia* fecundity (Fig. 4) across all months of the year. Sterner et al. (1997) also found that the month and temperature affected the slope of the relationship between light:TP and algal C:P. Therefore, we might expect seasonal differences in the effect of light:TP on zooplankton production. Although we found no significant change in the slope of the main effect between light:TP and *Daphnia* fecundity over time, we did find a strong seasonal effect of the environment on *Daphnia* fecundity (Fig. 6). This suggests that additional environmental variation (e.g., changes in solar irradiance, water mixing, algal community composition) causes seasonal differences in algal quality. At the phytoplankton community level, the concentration of blue-green algae negatively affects *Daphnia* reproduction (Demott 1999; Ferrao et al. 2000). We found a significantly negative effect of blue-green algae on *Daphnia* fecundity (Fig. 4), although not as strong as the light:TP effect (Table 2). It is therefore likely that the extent to which various aspects of food quality limit *Daphnia* production in Lake

Table 6. Values for twice the Schwarz criterion (2S) for the comparisons of DLM predictive models lacking a seasonal effect to season-only reference models for the long and short time series (from Tables 2, 4). Model numbers for the nonseasonal predictive models refer to those in Tables 3 (long) and 5 (short). See Table 2 for a description of the critical values for the Schwarz criterion.

Season-only	Nonseasonal predictive model									
	1	2	3	4	5	6	7	8	9	10
Long	47	40	35	28	27	26	16	15	12	3.5
Short	50	45	44	43	43	38	26	26	24	—

Washington varies with changes in phytoplankton community composition, which in turn varies within and across years (Schindler et al. 2001).

Most studies of the effect of algal quality on zooplankton reproduction have concentrated on lab experiments (e.g., Sterner et al. 1998) or comparative studies of different ecosystems (e.g., Brett et al. 2000; Dobberfuhl and Elser 2000). Testing hypotheses about the effects of food quality on zooplankton reproduction with time series of field data are rare. A 9-yr study of three hypereutrophic lakes in The Netherlands found an inverse relationship between algal quality (C:P ratio) and *Daphnia* abundance in two out of three lakes (Demott and Gulati 1999). The molar C:P ratio of the algae in the Dutch lakes ranged from 250 to 500 and were generally higher than the ~300 threshold, above which *Daphnia* production is expected to be constrained by food quality (Hessen 1992). Our prediction of algal C:P from light:TP based on the findings of Sterner et al. (1997) indicates values near or above the threshold (Fig. 3) and therefore support our result of a negative effect of light:TP on *Daphnia* fecundity.

In addition to algal quality, algal quantity directly affects zooplankton production. An increase in food concentration has caused increased *Daphnia* reproductive rates in the lab (Lynch 1989) and field (Wu and Culver 1994). Indeed, our time series analysis revealed a strong positive effect of algal quantity (Chl *a* concentration) on *Daphnia* fecundity (Fig. 4), both within and across years. When we combined Chl *a* and biovolume together, the observed effect of biovolume was negative and opposite of what we expected (Fig. 4). This could result from the residual effect of biovolume as a potential indicator of algal quality. However, we might expect that the other two direct measures of algal quality would outperform the more indirect residual effect of biovolume, but this was not the case. Alternatively, it could be an artifact of multicollinearity, whereby when two regression predictor variables are highly correlated, the observed sign of one of the coefficients is the opposite of the expected (Sokal and Rohlf 1995). Indeed, in our data set from Lake Washington, Chl *a* concentration and algal biovolume are strongly correlated (Pearson, $r = 0.88$, $P < 0.0001$).

Several possibilities exist for our observed difference in the negative effect of algal quality versus the positive effect of food quantity (Fig. 4). The smaller effect of the light:TP ratio on *Daphnia* fecundity, relative to the Chl *a* effect might reflect the relatively rapid uptake of soluble nutrients by algae compared to the response of *Daphnia* to changes in its food resource. Furthermore, we relied on the light:TP ratio as a metric of algal C:P (Sterner et al. 1997). However, other biochemical components of food quality, such as highly unsaturated fatty acids, can be important determinants of *Daphnia* growth (see review by Brett and Müller-Navarra 1997), and the relative importance of these fatty acids varies across phytoplankton P content and taxa (Sundbom and Vrede 1997). Furthermore, the relative importance of algal quality for zooplankton production may decrease with a decrease in algal quantity (Sterner 1997; Brett et al. 2000). This phenomenon occurs at low food abundance when a larger fraction of the energy consumed goes toward metabolism instead of growth. Finally, we observed a switch in the relative per-

formance of the algal quality versus quantity models in the analyses of the short time series (Table 5). However, we downplay this result because it likely reflects the loss of overall descriptive power when decreasing the sample size by 66% while introducing several missing values in the short time series.

Daphnia body size might also explain observed variation in fecundity due to allometry; larger individuals often have larger clutch sizes than smaller individuals (Peters 1983). Given that the size distribution of Daphnids is often highly variable (Lampert 1993), we might expect that variation in *Daphnia* length could explain the variation in fecundity over time. Lampert (1993) also found that fish predation caused a decrease in *Daphnia* size and subsequent fecundity over the summer. However, we found subtle seasonal differences in *Daphnia* length (Fig. 2). In fact, the slight increase in *Daphnia* length over the summer suggests weak predation effects by fish in Lake Washington. The unusual negative effect of *Daphnia* length on fecundity (Fig. 5) apparently resulted from the slight increase in *Daphnia* length from spring into late summer coincident with a substantial decrease in fecundity during the same time (Fig. 2). Thus we expect that this relationship is simply coincidental.

Daphnia did not become abundant in Lake Washington until 1977 (Edmondson and Litt 1982), but since then they have come to dominate the grazer community and exert strong control on their phytoplankton food resource (Edmondson 1994). Predicting the response of *Daphnia* to changes in its food quantity and quality is a critical part of understanding the food web dynamics in Lake Washington and other systems. By combining information on the physical, chemical, and biological characteristics of lakes in a temporally explicit framework, we were able to distinguish the effects of seasonal changes in the environment from other fundamental factors influencing *Daphnia* reproduction. By using formal time series analyses, we found considerable temporal organization in plankton dynamics that were not evident in a static representation of this system. This highlights the importance of temporal variation in algal quality and quantity effects on zooplankton production and suggests that simple experiments are conservative tests of these effects.

Predicting environmental stochasticity is nearly impossible, but we also found regular intra-annual patterns in the seasonal effects of the environment on *Daphnia* reproduction. At present, we do not know what the exact drivers of this seasonal forcing are, but temperature and day length are obvious factors. Ecosystems are not static, but rather change through time following changes in their various abiotic and biotic components, sometimes undergoing dramatic changes in their state (Scheffer et al. 2001). However, as we demonstrated here, some of this change is predictable across time. Our results should aid in future model formulation by offering insight into the temporal organization of ecosystem dynamics.

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Received: 7 January 2002

Accepted: 6 May 2002

Amended: 13 May 2002