

Weak density-dependence and short-term perturbations as determinants of phytoplankton temporal dynamics¹

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Abstract: We examined twelve temporal series of phytoplankton abundance in a diverse set of marine and freshwater habitats using semi-variogram analysis coupled with a stochastic discrete-time (daily) Gompertz model. The analysis revealed a very good correspondence between the theoretical semi-variogram function and the empirical semi-variograms. The estimated density-dependence parameters were remarkably similar in the various series and implied very weak regulation in phytoplankton abundance. Our results suggest that the magnitude of the daily variation in growth rates induced by density-independent factors increases with nutrient availability. The model also describes the general form of the mean-variance (temporal) relationship and is nearly identical to the empirical equation.

Keywords: phytoplankton, dynamics, semi-variogram, Gompertz, stochastic model, density-dependence.

Résumé: Nous avons étudié douze séries temporelles qui ont trait à l'abondance des populations phytoplanctoniques dans un ensemble d'habitats marins et d'eau douce, à l'aide d'une analyse des semi-variogrammes jumelée à un modèle stochastique de Gompertz en temps fini (quotidien). L'analyse a fait ressortir une bonne correspondance entre la fonction théorique du semi-variogramme et les semi-variogrammes empiriques. Les paramètres reflétant la dépendance à la densité étaient très similaires entre les séries, ce qui implique une très faible régulation des populations phytoplanctoniques. Les résultats indiquent que l'étendue des variations du taux de croissance nette associée à des facteurs indépendants de la densité augmente avec la disponibilité en éléments nutritifs. Le modèle décrit aussi la nature de la relation moyenne-variance (dans le temps) et il s'avère presque identique à l'équation empirique.

Mots-clés: phytoplancton, dynamique, semi-variogramme, Gompertz, modèle stochastique, densité-dépendance.

Introduction

The temporal dynamics of the total biomass of natural lake phytoplankton populations are traditionally depicted as a sequence of smooth waxes and wanes driven by the opposing forces of nutrient inputs and grazing control (Wetzel, 1983; Goldman & Horne, 1983; Sommer, 1986). Although heuristically appropriate, this approach has reinforced the simplified view that short-term fluctuations in algal abundance are but random noises superimposed on the main signal and researchers have consequently treated these fluctuations with little interest. However, there is mounting evidence that even rapid changes in population growth or decline may be the result of robust dynamic relationships between algae and zooplankton (McCauley, Murdoch & Watson, 1988; Murdoch & McCauley, 1985), and between algae and the available nutrient pool (Prairie & Marshall, 1995). Yet, with the many compartments of the pelagic food web interacting even at short time scales (Carpenter, 1988), regular and predictable properties of the temporal dynamics of algae have remained difficult to discern and characterize. Periodic oscillations are sometimes observed in experimental ponds (McCauley & Murdoch, 1987), but rarely in natural systems. Indeed, in the most comprehensive compilation of phytoplankton time-series assembled to date (Marshall &

Peters, 1989), even the supposedly 'omnipresent' spring and fall blooms of freshwater algae are but weak and inconsistent signals amidst the remaining fluctuations occurring throughout the year, particularly in oligotrophic waters (Sommer *et al.*, 1986). On the other hand, there is little doubt that phytoplankton biomass does not follow a purely indeterminate course. The key problem has been, and continues to be, the identification of general patterns in the dynamical behavior of phytoplankton, such as the presence and strength of density-dependent regulation (Murdoch, 1994).

Although the dynamics of phytoplankton have been studied on time scales ranging from short to long-term (Harris, 1980; 1986; Reynolds, 1984; 1990; Gaedke & Schweizer, 1993), the current view suggests that different processes predominate at different time scales. However, in spite of these real differences, the phytoplankton characteristically displays an apparently unique anti-persistent temporal signature (Prairie & Duarte, in prep.), suggesting that a single model may be sufficient to describe adequately at least some of the salient features of phytoplankton dynamics in most systems. In the case of stationary phenomena, anti-persistence is essentially synonymous with density-dependent population growth. Hence, phytoplankton temporal dynamics may be governed at least in part by density-dependent processes, the strength of which may be characteristic of

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these communities.

Here, we use a semi-variogram analysis to examine twelve temporal series of phytoplankton abundance obtained from a broad spectrum of aquatic habitats. The ecosystems were sampled at variable time resolution (days to weeks) and extent (one season to decades) and ranged from oligotrophic marine sites to eutrophic freshwater lakes. The two main goals were (i) to test whether consideration of density-dependence may reveal common key characteristics of the dynamics applicable to most systems, and (ii) whether these properties can be predicted on the basis of a single simple dynamical model. We felt that examining several algal communities would provide a better indication of the general prevalence of density-dependent regulation in these systems than a more detailed analysis of a single population (Murdoch, 1994).

Methods

DATA SOURCES

Temporal series of phytoplankton abundance (as measured by chlorophyll *a* concentrations) were assembled from various published and unpublished sources (Table I). Our choice of chlorophyll *a* as a measure of the abundance of the algal community was based on its widespread availability and good precision in its measurements. We recognize that it is an imperfect measure of abundance in that its concentration in algal cells is variable among taxa and can be influenced by light availability (Canfield, Linda & Hodgson, 1985). Nevertheless, we feel that it is the best variable available to test our hypotheses. The time-series varied in length (1 field season to 10 years) and in sampling frequency (daily to bi-weekly). Although some series were sampled at inconsistent sampling intervals, most series had a characteristic sampling frequency (daily, weekly, or bi-weekly). We accepted time-series whose lengths covered at least 65 times its characteristic sampling step, although the average time-series covered > 200 times its characteristic sampling interval. The ecosystems represented by the time-series cover a wide range of habitats, from the oligotrophic marine Bay of Blancs (northwest Mediterranean Sea) to small (Lake Brome, Québec) and large (Bodensee [Lake Constance], Germany-Switzerland-Austria) eutrophic lakes. In our analysis, we considered the three daily chlorophyll time-series obtained at different depths from Lake Cromwell (Québec) as inde-

pendent because of the strong vertical differentiation of their phytoplankton communities (Prairie, unpubl. data). A summary of the main characteristics of the time-series is given in Table I.

EMPIRICAL SEMI-VARIOGRAMS

We analyzed the structure of the time-series by constructing semi-variograms for each individual series. A semi-variogram is simply a plot of the (semi-)variance among observations distant by a time interval h as a function of h itself (see Robertson, 1987; Isaaks & Srivastava, 1989). Typically, semi-variograms are positive at short time scales (indicating that observations close in time are more similar than observations far apart in time), but the variance gradually reaches a plateau (the sill) corresponding to the maximum variance of the system (Figure 1). The time required to reach the sill is often referred to as the range of the semi-variogram and can serve as a useful measure of a characteristic time scale of the underlying process. For many empirical semi-variograms dealing with natural phenomena, although the semi-variance among measurements taken at time intervals h does increase with h , this variance is not nil when the trend is extrapolated to the origin (at $h = 0$). The semi-variance at $h = 0$ is referred to as the nugget variance (Figure 1), and is the combined result of natural variability phenomena (Prairie & Marshall, 1995), such as spatial heterogeneity, and measurement error (Isaak & Srivastava, 1989). Semi-

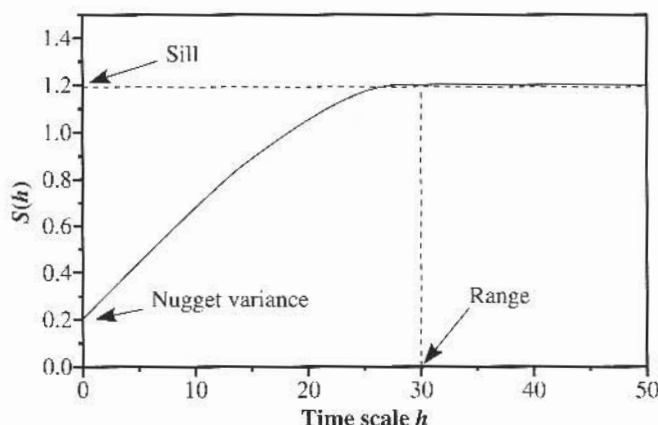


FIGURE 1. Example of a typical semi-variogram showing the maximum variance of the system (the sill), the nugget variance, and the range.

TABLE I. General characteristics of the time-series examined. * indicates marine systems. *N* is the number of observations

System	Sampling interval	Length of time-series	<i>N</i>	Mean (var) Chl <i>a</i> (μg/L)	Phosphorus (μg/L)	General characteristic	Source
Bay of Blancs*	Weekly	~ 3 years	243	0.84 (.755)	9.5	Oligotrophic marine bay	this study
L. Blue Chalk	Weekly	5 years	142	1.90 (4.25)	5	Mesotrophic lake	Marshall, 1987
Bodensee	Weekly	12 years	498	4.7 (31.8)	55	Large mesotrophic lake	unpubl. data
L. Brewer	Weekly	~ 5.5 years	141	26.7 (588)	60	Small eutrophic lake	Marshall, 1987
L. Brome	Weekly	~ 5 months	109	15.9 (246.5)	18	Small eutrophic lake	this study
Bay of Cadiz*	Bi-weekly	~ 19 years	330	1.85 (1.56)	45	Marine embayment	unpubl. data
L. Cromwell (0 m)	Daily	66 days	66	4.9 (4.3)	10	Small dystrophic lake	this study
L. Cromwell (1 m)	Daily	66 days	66	5.5 (6.0)	10	Small dystrophic lake	this study
L. Cromwell (2 m)	Daily	66 days	66	6.7 (12.4)	10	Small dystrophic lake	this study
Hamilton Harbour	Daily	~ 3 months	90	4.7 (6.45)	12	Mesotrophic embayment	Harris, 1987
L. Mcmphenmagog	Daily	135 days	135	3.3 (2.41)	13	Large mesotrophic lakes	Marshall, 1987
Tasmania*	Weekly	~ 3 years	127	1.51 (0.83)	17	Coastal	Clementson <i>et al.</i> , 1989

variograms contain much information about the temporal dynamics of a variable although the underlying dynamical process can only be deduced by inference or by comparison with theoretical semi-variogram functions derived from a model (see below). The empirical semi-variograms were computed on the \ln -transformed chlorophyll concentration data using the software GS+™ where each semi-variance value is calculated as

$$S(h) = \frac{1}{2N} \sum [\ln(P_{i+h}) - \ln(P_i)]^2 \quad [1]$$

Because the nugget variance represents variability induced by factors other than the underlying dynamical process, the estimated nugget variance was subtracted from all the semi-variance values of the corresponding time-series. Note that, although preferable, it is not necessary for the time-series to be sampled at a regular time interval. Semi-variogram analysis is particularly well suited to examine the dynamical behavior of time-series sampled with variable intensity. Nevertheless, we accepted only semi-variance values when obtained from 30 observation pairs or more, thereby insuring a sufficient robustness of the analysis.

THE MODEL

We developed a simple stochastic model purporting to reflect the dynamical process underlying changes in phytoplankton abundance. The model's performance was subsequently tested by deriving the theoretical semi-variogram function from the model, and then examining its correspondence with the empirical semi-variograms.

Given that one can reasonably assume the long-term mean abundance is fairly stable within lakes, the anti-persistent behavior of all the phytoplankton time-series examined by Prairie & Duarte (in prep.) clearly point to a mean-reverting process (Peters, 1994), which, for biological populations, is best conceived as density-dependent population growth. We therefore attempted to describe our time-series using one of the simplest and most flexible density-dependent models found in the literature. By flexibility, we imply a model that can display different strengths of density-dependence in growth. The model is a discrete-time difference equation of a first-order process known as the Gompertz model (Nisbet & Gurney, 1982) with a one day time step, and which relates population growth rate (R) to phytoplankton density (P) as a power function such that

$$R_t = \alpha P_t^{\beta-1} \quad [2]$$

where R_t is the population growth rate at time t (P_{t+1}/P_t), P_t is phytoplankton density (as mg Chlorophyll $a\ m^{-3}$) at time t and α and β are constants. Our choice of the time step (daily) was based on the short turnover time of most populations and on our interest in explaining short- to medium-term fluctuations. In addition, given the light dependence of photosynthetic activity, the daily interval seemed a natural discrete time step. Density-dependent growth occurs when $\beta < 1$ and the magnitude of the departure of β from unity increases with the strength of the density-dependence of population growth. We favored this model over the more popular logistic-type model because it allows for both weak and strong density-dependent forces. Objections have been

raised against this model on the grounds that the net population growth rate is theoretically unbounded (Royama, 1992). However, this concern is not always justified if the observed or predicted growth is always below the physiological maximum growth rate of the population examined. In logarithmic form and given that $R_t = P_{t+1}/P_t$, this model can be expressed as the linear equation

$$\ln(P_{t+1}) = \ln(\alpha) + \beta \ln(P_t) \quad [3]$$

the form of which can be recognized as analogous to a Ricker-type model where the log population abundance at one time step is a linear function of the previous log abundance. In this pure density-dependent process, the population reaches asymptotically a stable abundance value of $e^{-\ln(\alpha)/\beta}$ more or less rapidly depending on the exact value of β . As such, the model will be unrealistic in that no phytoplankton population has ever been observed to remain truly stable but rather displays large fluctuations and often aperiodic cycles. Indeed, most chlorophyll time-series show erratic trajectories in both the short and medium terms (Marshall & Peters, 1989). We thus postulate that the log growth rate would not only be a function of density but also of other factors which can collectively be represented by a stochastic and, we assume, Gaussian perturbation term u ($N[0, \text{var}(u)]$) such that

$$\ln(R) = \alpha' + (\beta - 1) \ln(P_t) + u_t \quad [4]$$

or

$$\ln(P_{t+1}) = \alpha' + \beta \ln(P_t) + u_t \quad [5]$$

where α' is $\ln(\alpha)$. The variance in u ($\text{var}(u)$) is a measure of the range within which daily population growth rate can vary due to factors other than the density-dependent process. The model can be expanded to yield a stochastic equation describing population density at any future step in time (see Royama, 1992) as

$$E[\ln(P_{t+h})] = \ln(P_t) \beta^h + E\left[\frac{(1-\beta^h)}{1-\beta}(\alpha' + u)\right] \quad [6]$$

If this model is an adequate representation of the process generating phytoplankton dynamics and assuming $\beta < 1$, then several general properties of the ensuing time-series can be predicted *a priori*:

- (1) the frequency distribution of the observed phytoplankton abundances will be log-normal,
- (2) the long-term mean for the \ln -transformed phytoplankton abundance will be stable at

$$E[\ln(P_t)] = \frac{-\alpha'}{\beta - 1} \quad [7]$$

and for the raw values at

$$E(P_t) = e^{\frac{-\alpha'}{\beta-1}} e^{\frac{\text{var}(u)}{2(1-\beta^2)}} \quad [8]$$

- (3) the long-term variance for the log-transformed phytoplankton abundance will be

$$\text{var}[\ln(P_t)] = \frac{\text{var}(u)}{1-\beta^2} \quad [9]$$

or for the raw data

$$\text{var}(P_t) = e^{\left(\frac{2\alpha'}{1-\beta}\right)} e^{\left(\frac{\text{var}(u)}{1-\beta^2}\right)} [e^{\left(\frac{\text{var}(u)}{1-\beta^2}\right)} - 1] \quad [10]$$

(4) the model allows one to predict the exact shape of the semi-variogram resulting from the model. For our model (equation 5) the theoretical semi-variogram function $S^T(h)$ of the \ln -transformed data can be derived to be

$$S^T(h) = \frac{\text{var}(u)}{1-\beta^2} (1 - e^{h \ln(\beta)}) = \frac{\text{var}(u)}{1-\beta^2} (1 - \beta^h) \quad [11]$$

where h is the time-step (days). Equation 11 can be recognized as an exponential semi-variogram function commonly used in the geostatistical literature (Isaak & Srivastava, 1989) for

which the sill is reached asymptotically. The practical range of an exponential semi-variogram function (*i.e.*, the time scale at which 95% of the total variance is reached) can be calculated as $\ln(0.05)/\ln(\beta)$. To illustrate the diversity of dynamical behavior the Gompertz model is capable of generating, we used equation 5 to simulate 4 year-long time-series with different strengths of density-dependence (β -values of 0.3, 0.5, 0.7, and 0.9) and a constant $\text{var}(u)$ parameter. The model can produce quite diverse time-series (Figure 2), with the characteristic time scale (as given by the range of the corresponding semi-variogram, Figure 2) increasing as the extent of density-dependence relaxes.

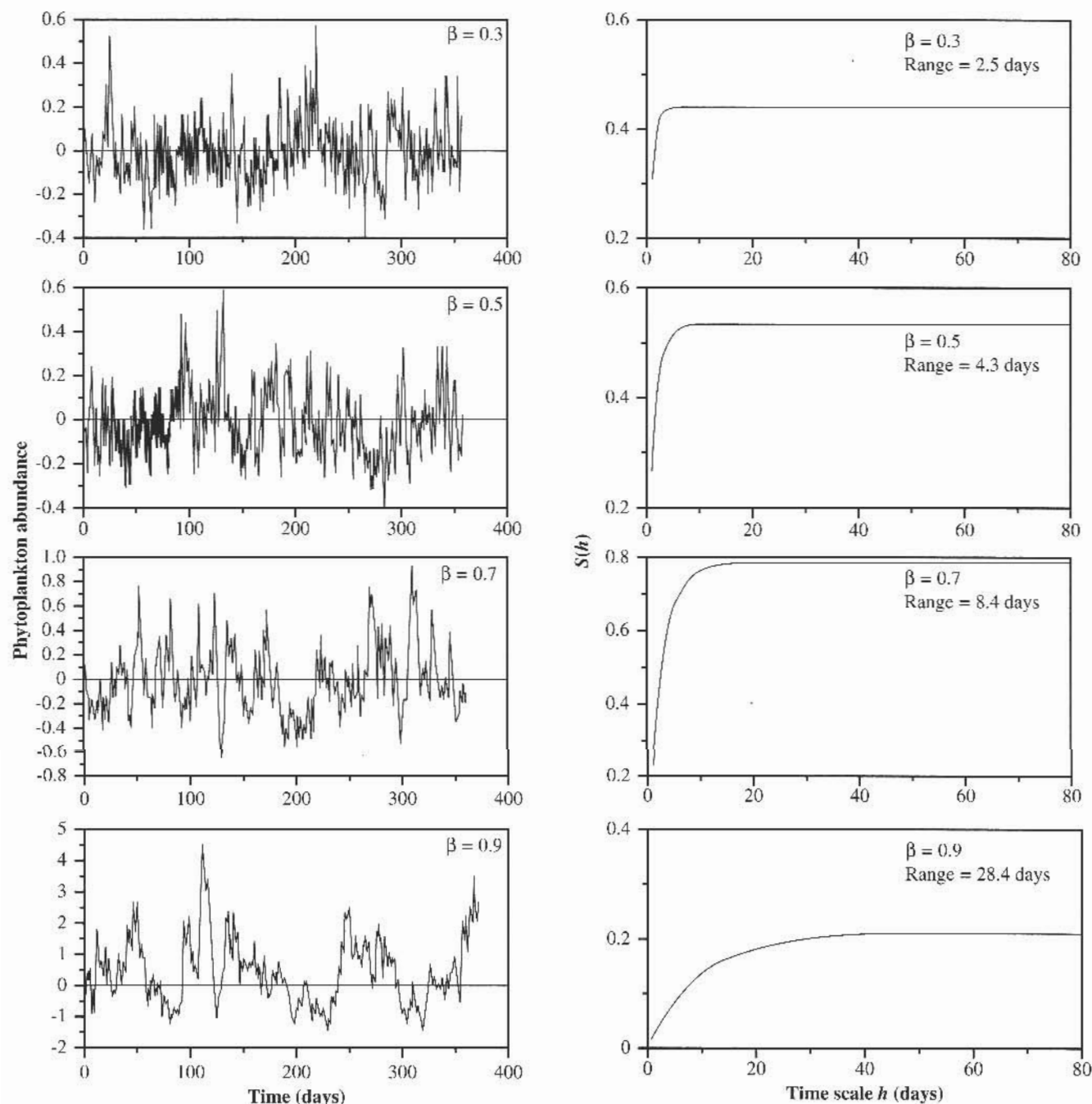


FIGURE 2. Simulated time-series (centered) and their corresponding theoretical semi-variogram function (equation 11) generated from the model equation 5 for 4 values of β (0.3, 0.5, 0.7, and 0.9) and an arbitrary but constant value of $\text{var}(u)$ (0.04).

MODEL TEST

Models such as equation 5 are typically tested by examining the fit of a regression of $\ln P_{t+1}$ on $\ln P_t$ or its analog, a regression of $\ln r_t$ on $\ln P_t$. However, the statistical detection of density-dependence is not an easy matter (Murdoch, 1994) and there are several known caveats to this approach: (1) even a very poor regression relationship between $\ln r_t$ and $\ln P_t$ does not necessarily indicate that the density-dependence is unimportant and (2) regressions based on ordinary least-squares will virtually always produce slope parameter estimates well below one even if the true underlying process (such as that produced in a simulation) is a pure random walk ($\alpha = 0$ and $\beta = 1$) (Royama, 1992). Although not widely recognized, this is essentially a problem of least-squares procedures and this downward bias could be corrected for using structural equation estimation techniques (Fuller, 1987; Prairie, Peters & Bird, 1995), but even those particularly suited for time-series analysis (Prairie & Marshall, 1995) may be difficult to apply in the present context because of the unstable error structure under various differencing values.

Instead, we tested the applicability of the model through its theoretical variogram function (equation 11), by examining the fit of this function to the empirical semi-variograms produced for each system. This allows for a very robust and sensitive test because small deviations in the observed *versus* predicted semi-variograms are readily apparent. Only two parameters are needed to fully describe the theoretical semi-variogram (equation 11): β and $\text{var}(u)$. Of these, $\text{var}(u)$ can be estimated empirically as the semi-variance at $h = 2$ (where $S[h] = \text{var}[u]$, see equation 11), which thus leaves only the strength of density-dependence (β) to be statistically fitted using standard non-linear least-squares techniques.

Results

GENERAL PROPERTIES

The time-series showed a wide array of temporal patterns ranging from relatively smooth curves (e.g., Lake Memphremagog) to erratic trajectories (e.g., Cadiz) (Figure 3). Mean chlorophyll values ranged from 0.8 to 27 $\mu\text{g/L}$ with temporal variance varying from 0.75 to 588 (Table I). For 3 of the time-series (Lake Cromwell 0 m, 1 m, and 2 m), the chlorophyll time-courses were clearly not stationary. As this will greatly bias the shape of the semi-variogram, these data were detrended from their linear component prior to the semi-variance analysis, a common remedial procedure in time-series analysis (Fuller, 1976).

As a first qualitative test of the model, we examined whether the frequency distribution of the phytoplankton abundances followed the predicted log-normal distribution. As a rule, our data, as other studies have shown (Harris & Piccinin, 1980; Heyman, Ryding & Forsberg, 1984), were indeed much better described by a log-normal distribution rather than a symmetrical one (e.g., Bodensee and Tasmania, Figure 4). Although consistent with the prediction of the models, this agreement is but a very weak test. Semi-variogram analysis provides a much stronger validation.

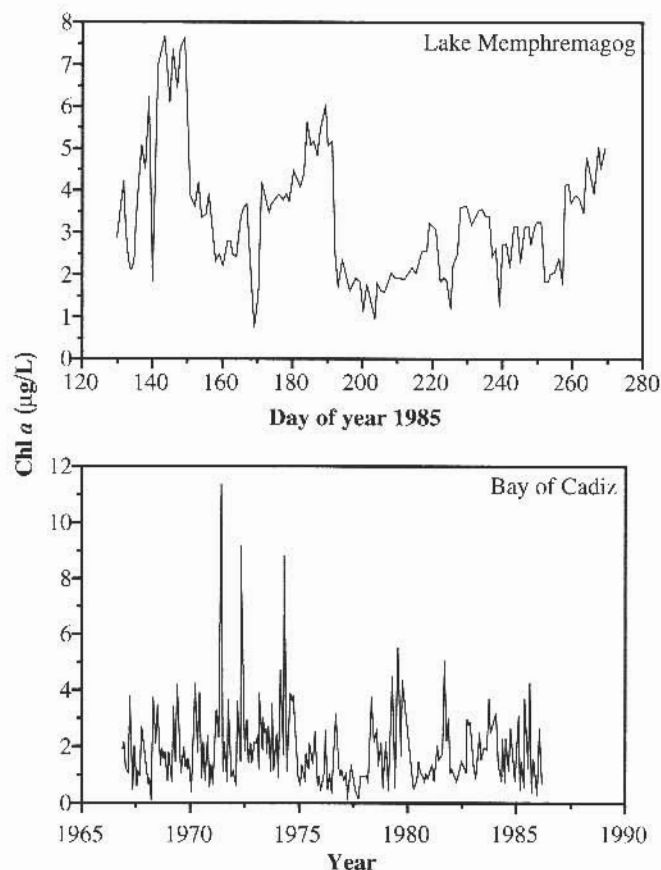


FIGURE 3. Two examples of the time-series examined in this study showing different temporal patterns.

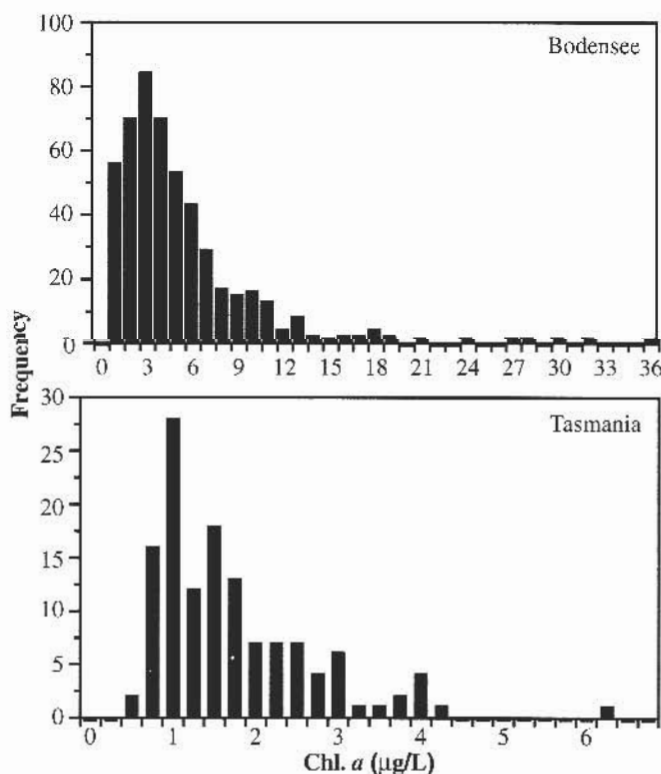


FIGURE 4. Frequency histograms of the chlorophyll *a* values from two systems showing a typical log-normal distribution.

SEMI-VARIOGRAMS

A visual examination of the semi-variograms shows that most time-series display the expected exponential model shape (Figure 5). The solid lines represent the function given by equation 11 for which $\text{var}(u)$ was the semi-variance value at $h = 2$ and β was statistically fitted using non-linear least-squares. Although the correspondence between theory and observation is generally adequate for most of our phytoplankton time-series examined, some systems exhibited a certain lack of fit. For example, the

model for Blue Chalk Lake clearly underestimated the variability at time-scales longer than 100 days. Similarly, the empirical semi-variogram for Lake Brome was more of the Gaussian than exponential type, with an inflexion point near the origin. In some cases, the semi-variances temporarily decreased passed the sill. The time-scale at which $S(h)$ is a minimum is indicative of the length of a periodic cycle. In our analysis, such apparently periodic components can be observed for the Bay of Blanes, Lake Cromwell (0 m), and Lake McPhremagog. However, it is doubtful that all can

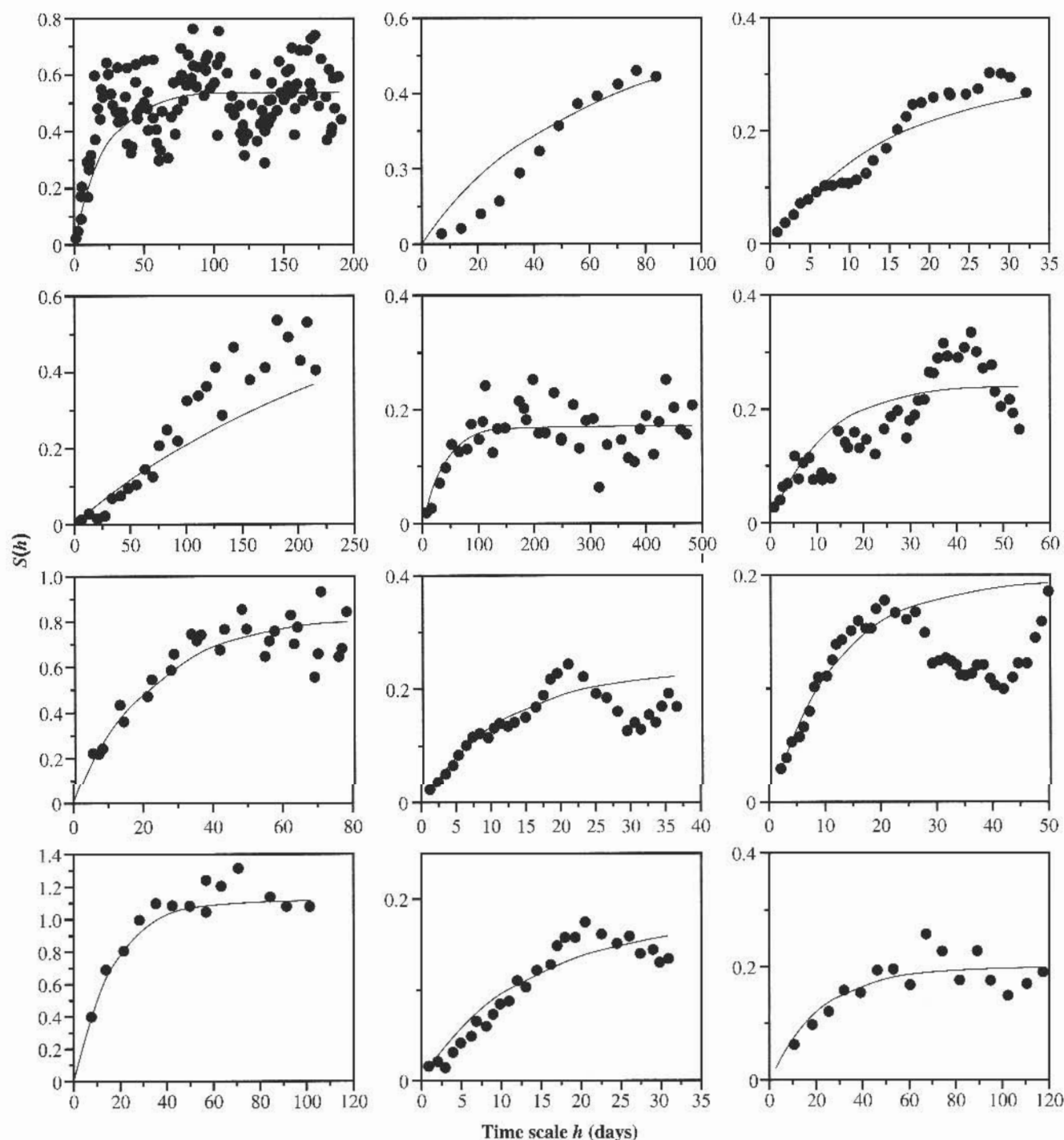


FIGURE 5. Temporal semi-variograms of the twelve time-series examined with the fitted theoretical semi-variogram function (equation 11).

be correctly interpreted as evidence for a periodic oscillation and probably a simple reflection of the short length of the time-series relative to the cycle length found. For example, the apparent cycle of period ~ 40 days in Lake Memphremagog (Figure 5) is clearly the result of only one such cycle within the 135 days of the time-series (Figure 3). Simulations (not shown) using time-series generated using equation 5 as the underlying model (*i.e.*, without any periodic component) show that such 'cycles' are very likely to be seen over relatively short runs of data. Under the same process but for long simulation runs however, these cycles are no longer apparent in the semi-variograms. This under-sampling artifact can account for the observed periodic component of the variograms for Lake Memphremagog and Lake Cromwell as they are both daily time-series based on only 135 and 66 observations, respectively. However, there appears to be a strong periodicity in the Bay of Blanes with a cycle length of about 60 days. In these cases, the theoretical semi-variogram functions are expected to capture only the mean trend once the sill is reached.

In general however, our model successfully reproduced key properties of the semi-variograms, such as the height of the sill relative to how quickly it is reached, a feature not very flexible in the theoretical semi-variogram function given that only one parameter (β) is fitted. Indeed, since $\text{var}(u)$ is empirically determined (from $S[h]$ at $h = 2$), equation 9 shows that the fitted parameter β must simultaneously depict both the maximum variance value (the sill) and the time necessary to reach it (the semi-variogram range, *i.e.*, $\ln[0.05]/\ln[\beta]$). Examination of the empirically determined $\text{var}(u)$, the fitted β parameter estimates and the semi-variogram ranges (Table II) reveals that the resulting β values were all high (close to 1) and similar in the different systems, ranging only between 0.92 and 0.99.

TABLE II. Estimated parameters β and $\text{var}(u)$ of the Gompertz model for the different time-series analyzed. The semi-variogram range is calculated as $\ln(0.05)/\ln(\beta)$ and is in days

System	β	$\text{var}(u)$	Range (days)
Bay of Blanes	0.943	0.061	51
L. Blue Chalk	0.996	0.005	> 2 years
Bodensee	0.956	0.070	67
L. Brewer	0.940	0.13	48
L. Brome	0.982	0.020	165
Bay of Cadiz	0.976	0.0079	123
L. Cromwell (0 m)	0.917	0.037	35
L. Cromwell (1 m)	0.925	0.030	38
L. Cromwell (2 m)	0.935	0.037	45
Hamilton Harbour	0.914	0.038	33
L. Memphremagog	0.920	0.03	36
Tasmania	0.956	0.017	67

FACTORS INFLUENCING $\text{var}(u)$ AND THE APPARENT STRENGTH OF DENSITY-DEPENDENCE (β)

The variance in u in our model is a measure of the magnitude by which factors other than density-dependence can affect daily community growth rate. In our analysis, the observed $\text{var}(u)$ ranged over 25 fold, with the highest value (0.13) found in the most eutrophic system (Lake Brewer) and the lowest (0.005) in the most oligotrophic lake (Lake Blue Chalk). Although this clearly suggests a relationship

with trophy, a log-log scatter plot of $\text{var}(u)$ versus mean chlorophyll was not significant. However, when we examined the relationship with a measure of the available nutrient pool (total phosphorus concentration), we found a clearer trend except for the Bay of Cadiz (Figure 6a). We suspect that this site behaved differently from the others because the phytoplankton there is not phosphorus-limited given that most (> 80%) of the phosphorus is dissolved (A. Gómez, pers. comm.). Although more data are necessary to confirm this pattern, our results suggest that the size of the available nutrient pool may play a role in determining the possible extent of variation in daily population growth.

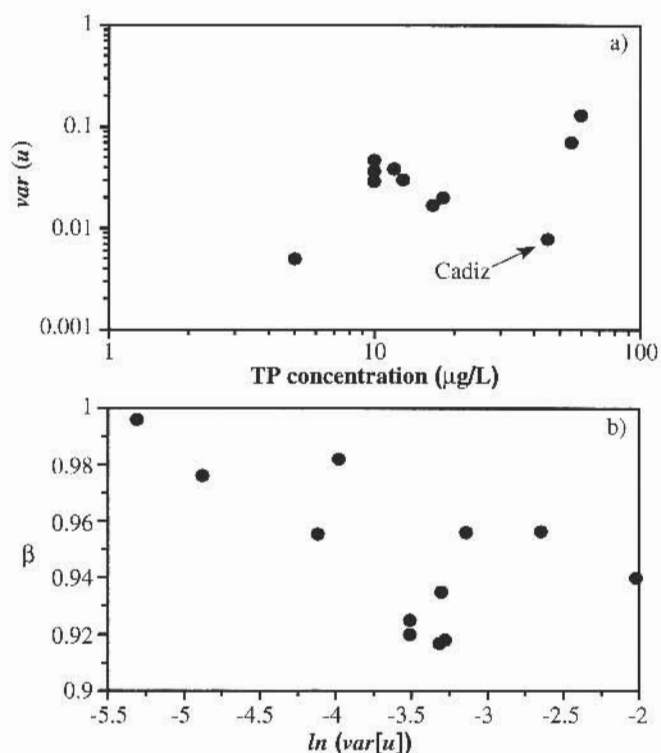


FIGURE 6. a) Scatter plot of $\text{var}(u)$ versus total phosphorus concentration (mg/L) (log-log scale). b) Scatter plot of the estimated β parameters and $\ln(\text{var}(u))$.

Although our analysis shows a remarkably narrow range in the estimated β parameter, the great precision afforded by the semi-variogram technique permitted the examination of possible factors influencing the apparent strength of density-dependence. In particular, we found that our measure of the external variability in daily growth rate ($\text{var}(u)$) could explain 48% of the variability in the estimated β parameter (Figure 6b), so that increasing dependence of phytoplankton biomass on short-term environmental conditions relaxes the strength of density-dependence. Surprisingly, however, we found no relationship between β and the degree of eutrophication expressed as either chlorophyll or phosphorus concentrations.

Discussion

Our analysis of phytoplankton dynamics indicates that most phytoplankton time-series can be reasonably well

described by a single density-dependent model incorporating daily stochastic perturbations. Given that, without the random perturbation term, the model predicts a stable and constant abundance value, the fluctuations observed in phytoplankton series are, therefore, ultimately driven by these small but important daily stochastic fluctuations. Thus, unless the time-course of the fluctuations can themselves be forecasted, it is clear that the exact trajectory of phytoplankton abundance cannot possibly be predicted with accuracy. Nevertheless, because the characteristic signature of the temporal series is well-described by a unique, underlying density-dependent process, key features of the dynamics (such as the shape and extent of the temporal semi-variogram) can be predicted with reasonable accuracy and precision.

The remarkably consistent but weak nature of the density-dependence ($0.92 < \beta < 0.99$) is ecologically highly significant given that these systems harbor very different algal communities in environments as diverse as oligotrophic marine habitats and eutrophic freshwaters. Our analysis therefore suggests that, in spite of the manifest complexity of pelagic food webs, the temporal dynamics of at least one of its major components (phytoplankton) can be greatly simplified without an undue loss in empirical reality. It also indicates that the net balance of ecological interactions presumably underlying the density-dependent process (*i.e.*, the balance between top-down, bottom-up and physical controls) is fairly stable in aquatic ecosystems, despite clear differences in the actual communities living in the systems. For example, the algal community of the Bay of Blanes is tightly controlled by grazers (Mura *et al.*, 1996) while the dominantly blue-green algal community of Lake Brome is mainly controlled by nutrients (Prairie, unpubl. data). Each individual interaction may be strong when studied separately (*i.e.*, in controlled experiments) but collectively, the net control exerted by these multiple interactions appears rather weak. This feature is not readily compatible with the current view of strong cascading interactions in aquatic systems (Carpenter, 1988; McQueen, Post & Mills, 1986), but is similar to the case made by Strong (1984) regarding insect populations.

The narrow range in the strength of density dependence ($0.92 < \beta < 0.99$) also has implications for the characteristic time scales of variability in phytoplankton biomass. Since the β parameter is mathematically related to the semi-variogram range (*i.e.*, the time necessary to reach the sill of the semi-variogram), the narrow band of β coefficients we observed implies that full extent of the dynamical behavior of phytoplankton will typically occur within time scales of 30-50 days (Table II). These findings highlight the importance of both seasonal and subseasonal processes in controlling algal dynamics (Prairie & Marshall, 1995) and have considerable consequences for the design of phytoplankton sampling programmes, which should focus on these time scales.

The Gompertz equation (equation 1) used here is only one of many theoretical models displaying density-dependent control (Nisbet & Gurney, 1982 for a compilation) and it may be argued that a similar fit could have been obtained with several different models. On the contrary, our analysis suggests that the Gompertz model is unique in that other

models would typically impose a much stronger density-dependence upon the dynamics. Given our results, this is not an adequate representation of the underlying process for phytoplankton. For example, the strength of density-dependence of the popular logistic model (in discrete time) relative to the β parameter of the Gompertz model used here can be estimated as

$$\frac{d \ln(P_{t+1})}{d \ln(P_t)} = \frac{d \left[\ln(P_t) + r \left(1 - \frac{P_t}{K} \right) \right]}{d \ln(P_t)} = 1 - \frac{rP_t}{K} \quad [12]$$

where r is the intrinsic rate of growth (d^{-1}) and K the carrying capacity. When P_t hovers around the carrying capacity K , the strength of the density-dependence reduces to $1-r$ which for phytoplankton would be in the neighborhood of -0.5 to -1 (since $r = 1.5-2.0$, Reynolds *et al.*, 1975); these values are very far from unity (no density-dependence) and from our empirically estimated values of $0.92-0.99$. Furthermore, the theoretical semi-variogram for the logistic model would reach its sill ($> 95\%$) much too quickly (at lag $h \approx 2-3$ days) than is clearly the case for algal populations (Figure 5). Our results suggest that modelling phytoplankton dynamics using the logistic equation is likely a poor choice.

We found that nutrient levels were better correlated to the $var(u)$ parameter than the average algal biomass. Because the parameter $var(u)$ drives a large portion of the dynamics, our analysis indicates that, in addition to setting the average algal standing stock (particularly in lakes) (Dillon & Rigler, 1974; Smith, 1982), nutrient levels may play an important role in determining the extent to which daily population growth rate can vary and, consequently, the particular type of dynamical pattern the algal population will exhibit. This agrees well with the suggestion that even the small daily fluctuations in phosphorus concentration have demonstrable consequences on the temporal dynamics of phytoplankton (Prairie & Marshall, 1995). Further research should be conducted to test whether attributes of other pelagic components, such as the zooplanktonic community, can also help predict our model parameters $var(u)$ and β .

FURTHER PREDICTIONS FROM THE MODEL

Given the adequate performance of the simple density-dependent model in describing key features of the dynamics, we feel justified in extracting further predictions from it. For example, the work of Ives (1995) suggests that ecosystem resilience in stochastic systems can be defined as the ratio of the variance in population density to the variance in growth rate. The smaller the ratio, the greater the resilience of the system to environmental perturbation. This ratio can be easily computed for our model as

$$Resilience = \frac{e^{\left(\frac{var(u)}{1-\beta^2} \right)} - 1}{var(u)} \bar{P}^2 \quad [13]$$

clearly indicating that eutrophic systems are much less resilient than oligotrophic ones. It is interesting to note that

within our data set, the 3 marine sites had the highest calculated resilience.

A second prediction can also be derived from the model. Equations 8 and 10 allow the prediction of both the mean and the temporal variance of the arithmetic chlorophyll values. Mean-variance (log-log) relationships are important for the design of efficient sampling programmes and have been developed for several lake variables (Knowlton, Hoyer & Jones, 1984; Marshall, Morin & Peters, 1988; France & Peters, 1992) including chlorophyll concentrations. Combining equations 8 and 10 yields a theoretical mean-variance relationship of the form

$$\text{var}(P) = \left[e^{\left(\frac{\text{var}(u)}{1-\beta^2} \right)} - 1 \right] \bar{P}^2 \quad [14]$$

Substituting in this equation the median values for $\text{var}(u)$ and β derived from our analysis (0.03 and 0.94, respectively, see Table II), we obtain

$$\text{var}(P) = 0.29 \bar{P}^2 \quad [15]$$

almost identical to the empirical equation of Marshall, Morin & Peters; (1988) of $\text{var}(P) = 0.295 \bar{P}^{2.1}$. Given that $\text{var}(u)$ is predictable from nutrient concentrations but not mean chlorophyll concentrations (Figure 6a), equation 14 further suggests that the temporal variance in chlorophyll may be even better forecasted from the average nutrient concentration rather than from mean chlorophyll levels. This prediction remains to be empirically confirmed.

In summary, the 12 temporal series describing phytoplankton dynamics in very diverse systems examined in this study shared important similarities, that were derivable from a simple stochastic Gompertz model. The strength of density-dependence was very weak in all systems, leading to characteristic time-scales of phytoplankton dynamics of about 40-50 days, and suggesting that the net effect of multiple interactions between pelagic components results in a loose control of phytoplankton abundance. Although several properties of phytoplankton dynamics predicted from the model have been confirmed independently, others await empirical testing. We suggest that further research should focus on testing whether a similar model can also adequately describe the temporal dynamics of other biological components and how it may relate to the primary producers.

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Literature cited

- Canfield, D. E., S. B. Linda & L. M. Hodgson, 1985. Chlorophyll-biomass-nutrient relationships for natural assemblages of Florida phytoplankton. *Water Resource Bulletin*, 21: 381-391.
- Carpenter, S. (ed.), 1988. *Complex Interactions in Lake Communities*, Springer Verlag, New York.
- Clementson, L. A., G. P. Harris, F. B. Griffiths & D. W. Rimmer, 1989. Seasonal and inter-annual variability in chemical and biological parameters in Strom Bay, Tasmania. I. Physics, chemistry and the biomass of components of the food chain. *Australian Journal of Marine Freshwater Research*, 40: 25-38.
- Dillon, P. J. & F. H. Rigler, 1974. The phosphorus-chlorophyll relationship in lakes. *Limnology and Oceanography*, 28: 792-795.
- France, R. L. & R. H. Peters, 1992. Temporal variance function for total phosphorus concentration. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 975-977.
- Fuller, W. A., 1976. *An Introduction to Statistical Time-Series*. John Wiley, New York.
- Fuller, W. A., 1987. *Measurement Error Models*. John Wiley, New York.
- Gaedke, U. & A. Schweizer, 1993. The first decade of oligotrophication in Lake Constance. I. The response of phytoplankton biomass and cell size. *Oecologia*, 93: 268-275.
- Goldman, C. R. & A. J. Horne, 1983. *Limnology*. McGraw-Hill, New York.
- Harris, G. P., 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. *Canadian Journal of Fisheries and Aquatic Sciences*, 37: 877-900.
- Harris, G. P., 1986. *Phytoplankton Ecology. Structure, Function and Fluctuation*. Chapman and Hall, London.
- Harris, G. P., 1987. Time series analysis of water quality data from Lake Ontario: Implications for the measurement of water quality in large and small lakes. *Freshwater Biology*, 18: 389-403.
- Harris, G. P. & B. B. Piccinin, 1980. Physical variability and phytoplankton communities. IV. Temporal changes in the phytoplankton community of physically variable lake. *Archiv für Hydrobiologie*, 89: 447-473.
- Heyman, U., S. O. Ryding & C. Forsberg, 1984. Frequency distributions of water quality variables. Relationships between mean and maximum values. *Water Research*, 18: 787-794.
- Isaaks, E. H. & R. M. Srivastava, 1989. *Applied Geostatistics*. Oxford University Press, Oxford.
- Ives, A. R., 1995. Measuring resilience in stochastic systems. *Ecological Monograph*, 65: 217-233.
- Knowlton, M. F., M. V. Hoyer & J. R. Jones, 1984. Sources of variability in phosphorus and chlorophyll and their effects on use of lake survey data. *Water Resources Bulletin*, 20: 397-407.
- Marshall, C. T., 1987. Seasonal patterns in chlorophyll-a for temperate lakes. M.Sc. thesis, McGill University, Montréal, Québec.
- Marshall, C. T., A. Morin & R. H. Peters, 1988. Estimates of mean chlorophyll-a concentration: Precision, accuracy, and sampling design. *Water Resources Bulletin*, 24: 102-1034.
- Marshall, C. T. & R. H. Peters, 1989. General patterns in the seasonal development of chlorophyll a for temperate lakes. *Limnology and Oceanography*, 34: 856-867.
- McCauley, E. & W. W. Murdoch, 1987. Cyclic and stable populations: Plankton as paradigm. *American Naturalist*, 129: 97-121.
- McCauley, E., W. W. Murdoch & S. Watson, 1988. Simple models and variation in plankton densities among lakes. *American*

- Naturalist, 132: 383-403.
- McQueen, D. J., J. R. Post & E. L. Mills, 1986. Trophic relationships in freshwater pelagic systems. *Canadian Journal of Fisheries and Aquatic Sciences*, 43: 1571-1581.
- Mura, M. P., S. Agusti, P. del Giorgio, J. Gasol, D. Vaque & C. M. Duarte, 1996. Grazer control of phytoplankton in nutrient-poor NW Mediterranean littoral. *Marine Ecology Progress Series*, 130: 213-219.
- Murdoch, W. W., 1994. Population regulation in theory and practice. *Ecology*, 75: 271-287.
- Murdoch, W. W. & E. McCauley, 1985. Three distinct types of dynamic behavior shown by a single planktonic system. *Nature*, 316: 628-630.
- Nisbet, R. M. & W. S. C. Gurney, 1982. *Modelling Fluctuating Populations*. John Wiley & Sons, Chichester.
- Peters, E. E., 1994. *Fractal Market Analysis: Applying Chaos Theory to Investment and Economics*. John Wiley & Sons, New York.
- Prairie, Y. T. & C. T. Marshall, 1995. On the use of structure time-series to detect and test hypotheses about within lakes relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 799-803.
- Prairie, Y. T., R. H. Peters & D. F. Bird, 1995. Natural variability and the estimation of empirical relationships: A re-assessment of regression methods. *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 788-798.
- Reynolds, C. S., 1984. *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, Cambridge.
- Reynolds, C. S., 1990. Temporal scales of variability in pelagic environments and the response of phytoplankton. *Freshwater Biology*, 23: 25-53.
- Reynolds, J. H., E. J. Middlebrooks, D. B. Porcella & W. J. Grenney, 1975. Effects of temperature on growth constants of *Selenastrum capricornutum*. *Journal of the Water Pollution Control Federation*, 47: 2420-2436.
- Robertson, G. P., 1987. Geostatistics in ecology: Interpolating with known variance. *Ecology*, 68: 744-748.
- Royama, T., 1992. *Analytical Population Dynamics*. Chapman & Hall, London.
- Sommer, U., 1986. The periodicity of phytoplankton in Lake Constance (Bodensee) in comparison to other deep lakes of central Europe. *Hydrobiologia*, 138: 1-7.
- Sommer, U., Z. M. Gliwicz, W. Lampert & A. Duncan, 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie*, 106: 433-471.
- Smith, V. H., 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: An empirical and theoretical analysis. *Limnology and Oceanography*, 27: 1101-1112.
- Strong, D. R., 1984. Density-vague ecology and liberal population regulation in insects. Pages 313-327 in P. W. Price, C. N. Slobodchikoff & W. S. Gaud (ed.). *A New Ecology: Novel Approaches to Interactive Systems*. John Wiley & Sons, New York.
- Wetzel, R. G., 1983. *Limnology*. 2nd edition. Saunders, Philadelphia, Pennsylvania.