

Increased ecosystem variability and reduced predictability following fertilisation: Evidence from palaeolimnology

Kathryn L. Cottingham,¹ James A. Rusak^{2,3} and Peter R. Leavitt³

¹Department of Biological Sciences, Dartmouth College, 6044 Gilman Laboratory, Hanover, NH 03755–3576, U.S.A. E-mail: Kathryn.Cottingham@dartmouth.edu

²Department of Biology, York University, Toronto, ON M3J 1P3, Canada.

³Limnology Laboratory, University of Regina, Regina, SK S4S 0A2, Canada.

Abstract

We tested the hypothesis that fertilisation increases community and ecosystem variability while reducing predictability using annual fossil records from fertilised Lake 227, Experimental Lakes Area, Ontario, Canada. Comparison of fossil pigments from unperturbed and eutrophied periods using a median-log Levene's test demonstrated that variability increased significantly during enrichment for total algae (chlorophyll *a*, sum of carotenoids), cyanobacteria (aphanizophyll, lutein-zeaxanthin), chlorophytes (pheophytin *b*, lutein-zeaxanthin), and cryptophytes (alloxanthin), but not for other algal taxa (chrysophytes, dinoflagellates) or herbivory (pheophorbides). Dynamic linear models (DLMs) of individual time series showed that forecast accuracy declined during enrichment for taxa which showed increased variability, while forecast uncertainty increased for all fossil pigments. DLMs of simulated data identified a strong inverse relationship between variability and predictability, suggesting that predictability will decline whenever variability increases. These findings imply that anthropogenic eutrophication of ecosystems may destabilise lakes, obscure impacts of global change, and reduce the sensitivity of whole-ecosystem experiments.

Keywords

Dynamic linear models, ecosystem experiment, Experimental Lakes Area, fertilization, Lake 227, Levene's test, perturbation, predictability, time series, variability.

Ecology Letters (2000) 3: 340–348

INTRODUCTION

Ecologists have suggested for many years that perturbations increase the variability of ecological systems (Odum *et al.* 1979; Underwood 1991). Changes in temporal variability were first predicted on theoretical grounds, when Rosenzweig (1971) showed that the dynamics of a generalised predator–prey model are destabilised when enhanced nutrient availability increases prey carrying capacity. Although this 'paradox of enrichment' has been explored thoroughly in models (e.g. Yodzis & Innis 1992; Abrams & Walters 1996), empirical demonstrations of its existence in natural communities have been equivocal, in part because of the relative simplicity of Rosenzweig's model as compared to the complexity of natural systems (Scheffer & De Boer 1995; Murdoch *et al.* 1998). In contrast, spatial variation is known to increase in the benthic communities of many polluted aquatic systems (e.g. Warwick *et al.* 1990; Agard *et al.* 1993), leading to the

suggestion that increased variability may serve as an indicator of ecosystem perturbation (Underwood 1991; Warwick & Clarke 1993). Improved understanding of variance–fertility relationships is essential because human activities are increasing nutrient flux to many ecosystems (Vitousek *et al.* 1997; Carpenter *et al.* 1998), and because resultant increases in variability may reduce species diversity (Pimm *et al.* 1988) and obscure impacts of global climate change (Hulme *et al.* 1999).

In this paper, we use annually resolved palaeoecological records from a whole-lake fertilisation experiment (Schindler 1988) to test the hypothesis that enrichment increases the variance and reduces the predictability of the algal component of aquatic ecosystems. Palaeoecological data have many advantages, including good correlations between plankton and fossil abundance (e.g. Leavitt 1993; Leavitt & Findlay 1994; Leavitt *et al.* 1999), consistent methodology through time, and the ability to obtain equally long time series before and after perturbation (i.e.

a balanced design, which facilitates tests of variability–Keyes & Levy 1997). We also take advantage of two modern statistical techniques to quantify time series behaviour: a median-log Levene's test (Schultz 1985) to measure variability and dynamic linear models (West & Harrison 1997) to estimate ecosystem predictability.

MATERIALS AND METHODS

Palaeoecological data

Site description and history

Lake 227 is a 5-ha, 10 m deep, dilute headwater lake located in the Experimental Lakes Area (ELA) of north-western Ontario (49°2'N, 93°42'W). Lake chemistry, biology, experimental history, and palaeoecological analyses have been described elsewhere (Leavitt & Findlay 1994; Leavitt *et al.* 1994). Briefly, natural pelagic communities consisted of chrysophytes and cryptophytes, small-bodied zooplankton (*Bosmina*, *Diatomus*) and cyprinid fishes. Strong summer stratification (thermocline 2–4 m), incomplete turnover and an anoxic hypolimnion have produced annually laminated (varved) sediments throughout the last 400 years (Leavitt *et al.* 1994).

Lake 227 has been the subject of several well-documented experimental manipulations. Since 1969, the annual loading of phosphorus (P as Na₂HPO₄ or H₃PO₄) has been experimentally enhanced at approximately 10 × the background loading rate. From 1969 to 1974, P was added together with nitrogen (N as NaNO₃) at a moderate N:P ratio (14:1 N:P by mass), stimulating a four to five-fold increase in the standing crops of chlorophytes and colonial cyanobacteria (Findlay & Kling 1975; Leavitt & Findlay 1994). Beginning in 1975, the nitrogen loading was reduced three-fold to a 5:1 N:P ratio by mass, and blooms of N₂-fixing cyanobacteria (*Aphanizomenon*) replaced chlorophytes as the predominant algae through 1982. More recently, the phytoplankton community has alternated between periods of chlorophyte and cyanobacterial dominance (Leavitt & Findlay 1994).

Sediment analyses

Palaeoecological analyses of Lake 227 have been detailed elsewhere (Leavitt *et al.* 1994 and references therein). Annual laminae were isolated and analysed for fossil pigment content by standard high performance liquid chromatography (Leavitt & Findlay 1994). Concentrations of sedimentary carotenoids, chlorophylls, and derivatives (nmoles pigment·g⁻¹ organic matter) were quantified for each year between 1943 and 1990 (Fig. 1) and for 14 additional years between 1793 and 1940.

Fossil pigments recorded many, but not all, major changes in the phytoplankton community resulting from

experimental whole-lake eutrophication (Leavitt & Findlay 1994). Concentrations of fossil pigments were most strongly correlated to annual phytoplankton standing crops (mg wet wt·m⁻²) and summarised phytoplankton community change in taxonomic units equivalent to algal functional groups (Table 1; Leavitt & Findlay 1994). Plankton–fossil correlations were similar among pigments and hard fossils of algae (Leavitt & Findlay 1994; Leavitt *et al.* 1994) and were strongest ($r = 0.27$ – 0.65) for algae whose abundance was greatest during the limnological sampling period (May–Oct) and which had negligible benthic populations (e.g. colonial cyanobacteria).

We analysed the variability and predictability of 10 algal pigments: eight at the community level (fucoxanthin, alloxanthin, lutein-zeaxanthin, echinenone, myxoxanthophyll, aphanizophyll, chlorophyll *b*, pheophytin *b*) and two at the ecosystem level (β -carotene, chlorophyll *a*). In addition, we analysed an aggregate pigment variable, the sum of algal indicator carotenoids (alloxanthin, fucoxanthin, lutein-zeaxanthin, myxoxanthophyll, aphanizophyll) for ecosystem variability only. Finally, we analysed two pigments that indicate relative levels of herbivory (pheophorbides *a* and *b*).

Variability

We compared interannual variability before and during experimental enrichment using the median-log Levene's test for homogeneity of variance (e.g. Schultz 1985). In this procedure, we log₁₀-transformed each time series to control variance as a function of mean (cf. Underwood 1997), then scaled the variance to the median of the period of interest and calculated Levene's test via a one-way analysis of variance. Prior to analysis, we eliminated transition years (1966–68) to reduce impacts of incomplete isolation of individual sediment laminae (Leavitt & Findlay 1994) and to ensure a balanced design when comparing prefertilization (1944–65) and enrichment periods (1969–90) (cf. Keyes & Levy 1997). Finally, we replaced a known outlier for pheophorbide *a* in 1960 with the grand mean of the adjusted time series; this manipulation did not affect our conclusions (see below).

Predictability

The predictability of the Lake 227 algal community was quantified using dynamic linear model (DLM; West & Harrison 1997) analysis of fossil pigment time series. DLMs were created to deal with complex systems that change through time—i.e. systems for which conventional, fixed-parameter models do not work well (Lamon *et al.* 1998). There are two equations for each DLM: an observation eqn 1 relating observations at time t (Y_t) to

Pigment Time Series

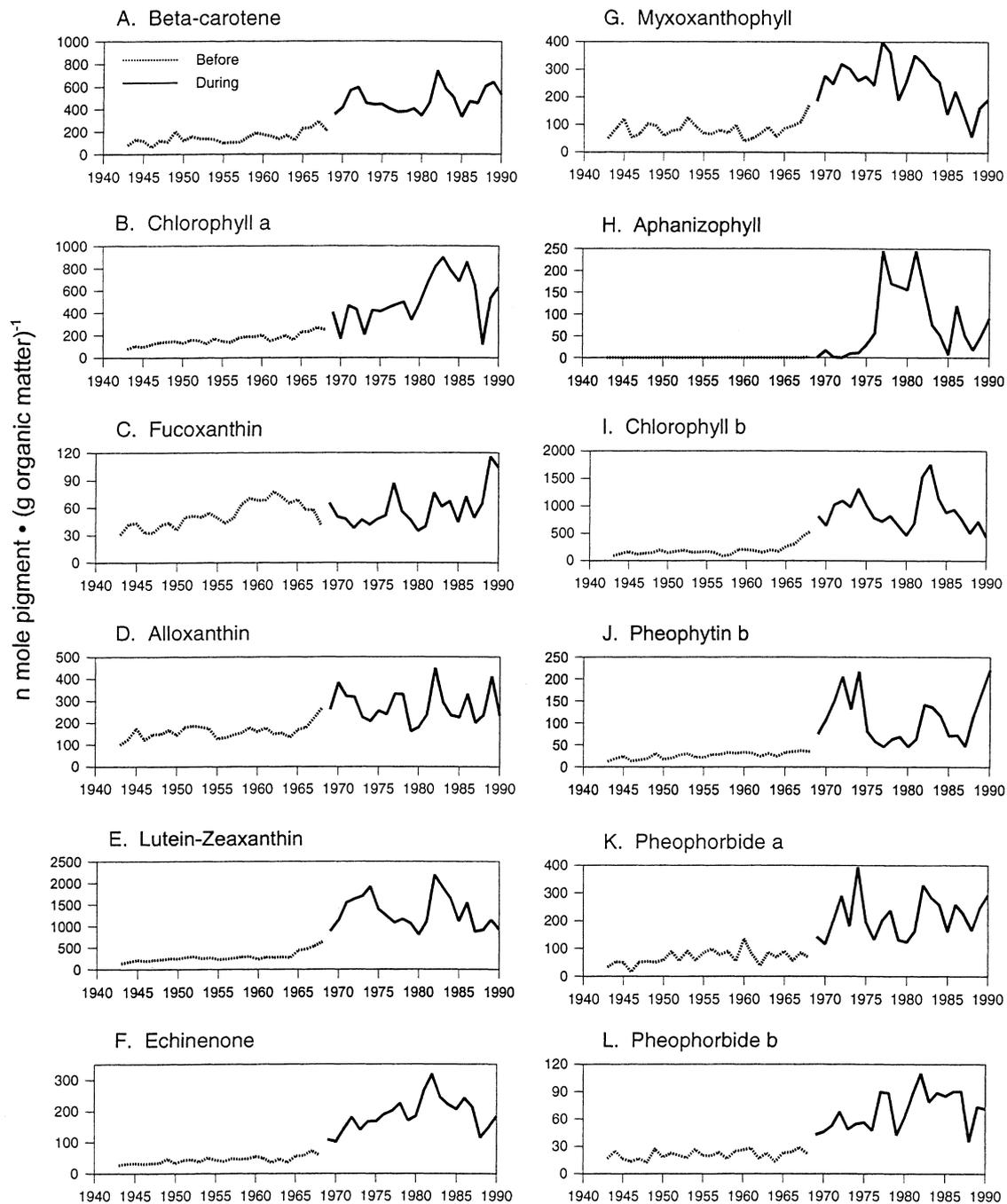


Figure 1 Time series for fossil pigments from Lake 227, Ontario. A, β -carotene. B, Chlorophyll *a*. C, Fucoxanthin. D, Alloxanthin. E, Lutein-zeaxanthin. F, Echinenone. G, Myxoxanthophyll. H, Aphanizophyll. I, Chlorophyll *b*. J, Pheophytin *b*. K, Pheophorbide *a*. L, Pheophorbide *b*.

parameters (μ_t), and a system eqn 2 describing the evolution of parameters (μ_t) through time:

$$Y_t = \mu_t + v_t \quad v_t \sim N[0, V_t] \quad (1)$$

$$\mu_t = \mu_{t-1} + \omega_t \quad \omega_t \sim t_{n_t-1}[0, W_t] \quad (2)$$

In eqn 1, v_t is the observation variance which is normally distributed with mean 0 and variance V_t .

Table 1 Correspondence of fossil pigments to extant taxa, based on Leavitt & Findlay (1994) and correlations between observed values and one-step-ahead predictions from the DLMs

Pigment	Corresponding taxa	DLM correlation
Beta-carotene	All algae	0.89
Chlorophyll <i>a</i>	All algae	0.81
Fucoxanthin	Diatoms, chrysophytes, some dinoflagellates	0.53
Alloxanthin	Cryptophytes	0.66
Lutein-zeaxanthin	Cyanobacteria, chlorophytes	0.87
Echinenone	All cyanobacteria	0.92
Myxoxanthophyll	Colonial cyanobacteria	0.83
Aphanizophyll	N ₂ fixing cyanobacteria	0.64
Chlorophyll <i>b</i>	Chlorophytes	0.82
Pheophytin <i>b</i>	Chlorophytes	0.69
Pheophorbide <i>a</i>	Herbivory	0.67
Pheophorbide <i>b</i>	Herbivory	0.86

In eqn 2, ω_t is the evolution variance which has a Student *t* distribution with mode 0 and scale matrix W_t . The error terms v_t and ω_t are assumed to be temporally and mutually independent. We used Bayesian learning to estimate μ_t and V_t . W_t and some aspects of V_t were incorporated through discount factors which were determined separately for each time series.

We used a simple one parameter DLM with discount factors to maximize model fit. Variance intervention (see appendix in Cottingham & Carpenter 1998) was used to increase model adaptability during the period of greatest change (1966–73). The mean and variance of all observations prior to 1943 ($n = 14$) provided an estimate of the prior mean and variance. Cottingham & Carpenter (1998) provide further details on the adaptation of standard DLMs to ecological time series.

Ecosystem predictability was assessed by comparing DLM forecasts with observed fossil pigment abundance during both unperturbed and enriched periods. After each year, model parameters were updated and used to forecast the level and 90% highest posterior density (HPD) intervals for the next five years of the time series. Prediction errors were calculated as the percent error between observations and predictions for intervals of 1–5 years. Mean percent errors (MPE) for the unperturbed (1944–65) and enriched (1969–90) periods were then calculated and compared using the Mann–Whitney *U*-test ($\alpha = 0.05$) for each prediction interval. Accuracy of the predictions was said to have decreased if MPE increased significantly during the enrichment period. Similarly, prediction uncertainty was considered to have increased if the mean width of 90% HPD intervals during enrichment was significantly greater (Mann–Whitney *U*-test, $\alpha = 0.05$) than those of the unperturbed period.

Simulation study

To better quantify the statistical relationship between variability and predictability measured with DLMs, we constructed a set of simulated data with fixed coefficients of variation (CV), then determined the predictability of each simulated time series. In these analyses, we do not attempt to duplicate the shift in variability in Lake 227 in response to enrichment, but rather explore correlations between known variability and calculated predictability of time series. We simulated time series with 40 observations selected randomly from a normal distribution with a mean of 20 and a variance corresponding to one of 14 fixed standard deviations between 2 and 36; consequently, the simulated series have CV's comparable to those in our palaeoecological records (0.1–1.8). After all data were simulated, we added a constant value to each observation to ensure that no points had values less than 0. Ten replicate data sets were generated for each standard deviation, yielding a total of 140 simulated time series.

Predictability was determined using a modification of the procedure described above. For each simulated time series, we used data points 1–10 to determine the prior mean and variance, then fit a DLM to data points 11–40. Mean prediction error and mean uncertainty for one-step-ahead predictions were determined for observations 11–40. Finally, we used simple linear regression to determine whether simulated CV was a significant ($\alpha = 0.05$) predictor of prediction accuracy or uncertainty.

To test whether the nominal mean had a significant effect on observed relationships, we repeated this simulation study for means of 20, 50, 100, 500, 1000 and 1500. Because the qualitative results were similar regardless of the mean used, we report only the simulations with mean = 20.

RESULTS

Palaeoecological data

Variability

Analysis with the median-log Levene's test indicated that lake fertilisation resulted in increased variability of pigments from cryptophytes (alloxanthin), chlorophytes (lutein-zeaxanthin, pheophytin *b*), and cyanobacteria (lutein-zeaxanthin) (Fig. 2). We also infer that the variability of N-fixing cyanobacteria (aphanizophyll) increased with enrichment, since this pigment was absent before enrichment and present (but quite variable) during enrichment (Fig. 1). In contrast, time series representing chrysophytes and dinoflagellates (fucoxanthin), total cyanobacteria (echinenone), colonial cyanobacteria (myxoxanthophyll), and grazing by herbivores (pheophorbides *a* and *b*) showed no significant change in variability (Fig. 2). Furthermore, the variability

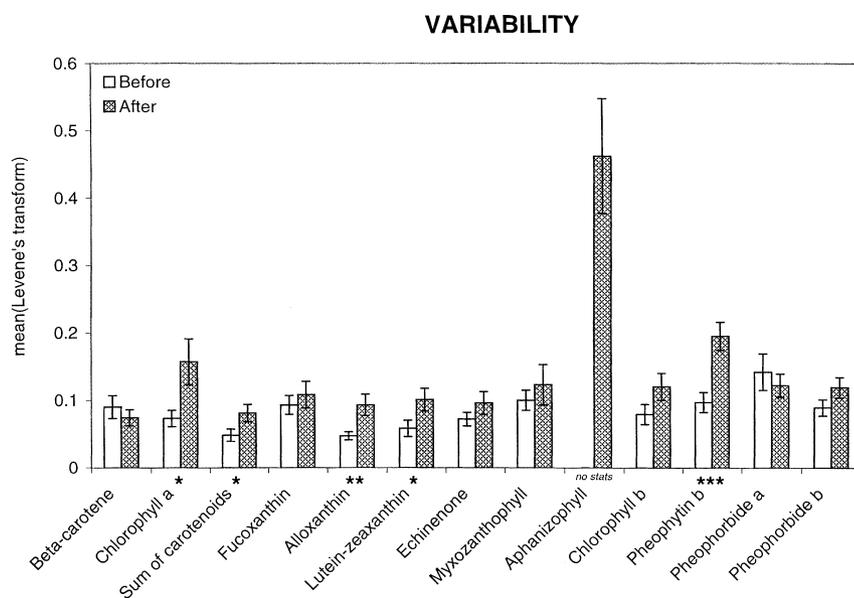


Figure 2 Fossil pigment time series variability based on the median-log Levene's test for the periods before (open bars) and during (hatched bars) experimental nutrient enrichment. Each bar indicates the mean Levene's transform \pm 1 SE. All *P*-values are indicated by asterisks below the appropriate pair of bars: * for $P \leq 0.05$, ** for $P \leq 0.01$, and *** for $P \leq 0.001$; absence of asterisks indicates that the comparison was not significant at $\alpha = 0.05$.

of total algal abundance increased when measured using the chemically labile pigment chlorophyll *a* and the sum of algal indicator carotenoids (alloxanthin, fucoxanthin, lutein-zeaxanthin, myxozanthophyll, aphanizophyll), but not when chemically stable β -carotene was analysed. Because the median-log Levene's test is robust to mean–variance correlations, we infer that observed patterns reflect true differences in algal variability rather than artefacts related to the magnitude of biomass change. In addition, preliminary analyses from an unmodified reference lake (Lake 302S 1945–80; Leavitt *et al.* 1999) suggest that it is unlikely that there were significant increases in fossil variability (1969–80) independent of fertilization.

Predictability

DLMs fit all fossil time series well, as indicated by significant correlations between observed pigment concentrations and values predicted in the previous year ($r = 0.53$ – 0.92 , $n = 43$; Table 1). Similarly, residuals from model fits were all normally distributed.

Prediction accuracy declined (MPE increased) for the pigments which exhibited significant increases in variability (chlorophyll *a*, alloxanthin, lutein-zeaxanthin, pheophytin *b*, sum of algal indicator carotenoids), plus chlorophyll *b* (Fig. 3). Reductions were significant ($P < 0.05$) for all prediction intervals, except for chlorophyll *a* with intervals of 1 or 3 years. Prediction accuracy for aphanizophyll (N_2 -fixing cyanobacteria) was inferred to have declined with ecosystem enrichment, although the baseline MPE could not be calculated because the pigment was always absent prior to 1970 (Fig. 1).

Prediction uncertainty increased during enrichment for all fossil pigments (Fig. 3). This result was not a

methodological artefact due to the variance intervention, as the postenrichment uncertainty was even greater if the variance intervention was not included (data not shown).

Simulated data

Analysis of simulated data suggests that increased variability will always lead to decreased accuracy and increased uncertainty when predictability is assessed using DLMs. Both the inaccuracy (MPE) and uncertainty of DLM predictions increased significantly with increased variability (CV), regardless of the time series mean (Fig. 4).

DISCUSSION

Our analyses support the hypothesis that fertilisation increases algal community variability while reducing the predictability of future change. Interannual variability increased and predictability declined for pigments characteristic of cryptophytes (alloxanthin), chlorophytes (pheophytin *b*, lutein-zeaxanthin) and N_2 -fixing cyanobacteria (aphanizophyll, lutein-zeaxanthin), but not for siliceous algae (fucoxanthin) or nonheterocystous cyanobacteria (echinenone, myxozanthophyll). Increased variance was unrelated to the magnitude (as percentage of baseline) of biomass increase following fertilization, since alloxanthin (180%) was substantially less responsive to fertilisation than were either echinenone or myxozanthophyll ($> 325\%$; Fig. 1; Leavitt *et al.* 1994). Instead, heightened variability was observed for total algal abundance (chlorophyll *a*, sum of algal indicator carotenoids) as well as algae which were biomass-dominants in phytoplankton during some part of the time series (pre- or

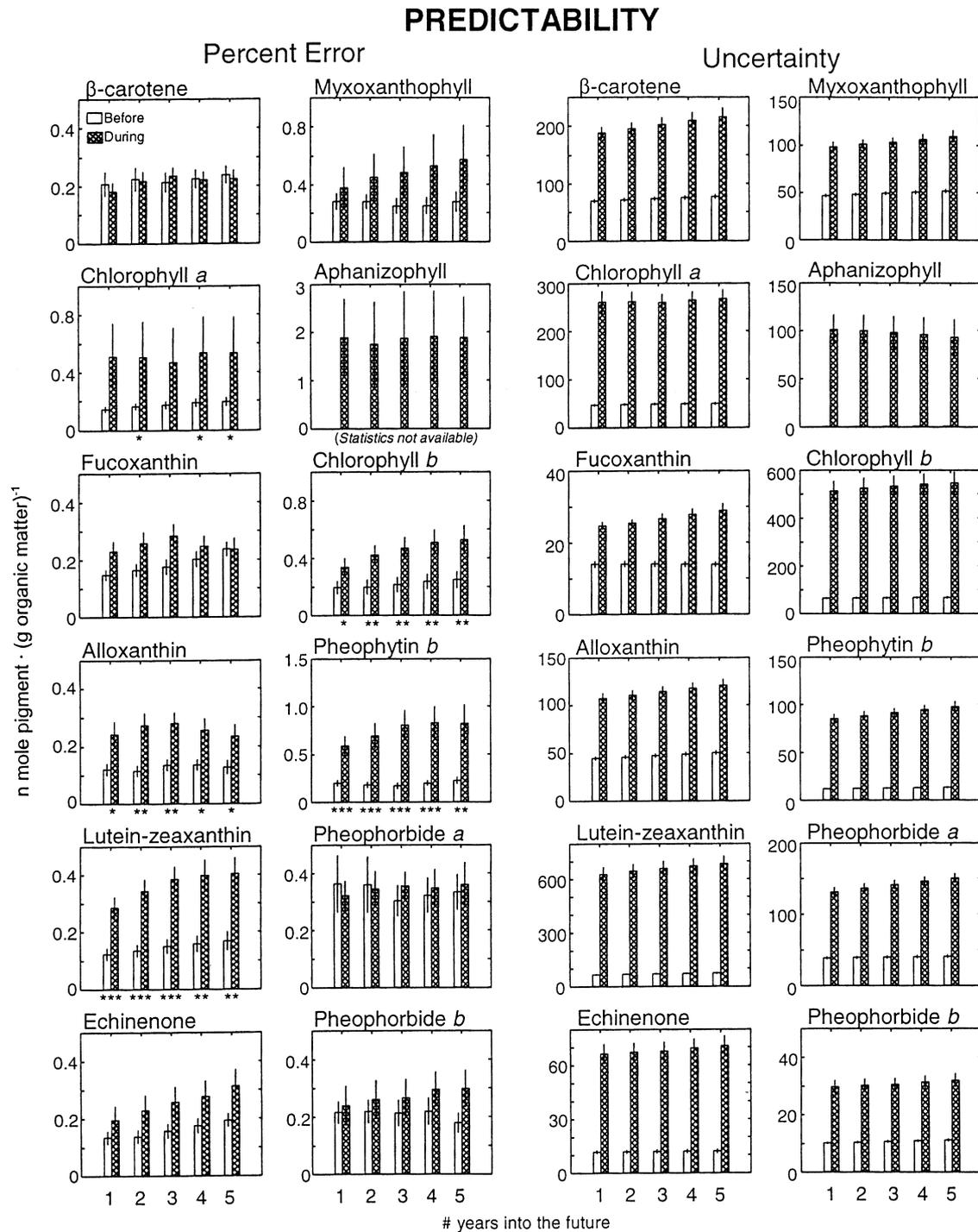


Figure 3 Fossil pigment time series predictability based on dynamic linear model forecasts (1–5 years) for the periods before (open bars) and during (hatched bars) enrichment. Inaccuracy was evaluated using mean percent error (MPE; first two columns), while uncertainty was evaluated using mean width of the 90% HPD intervals (third & fourth columns). Each bar indicates the mean ± 1 SE; we compared these means using the Mann–Whitney U -test. All P -values are indicated by asterisks below the appropriate bars: * for $P \leq 0.05$, ** for $P \leq 0.01$, and *** for $P \leq 0.001$; absence of asterisks indicates that the comparison was not significant at $\alpha = 0.05$.

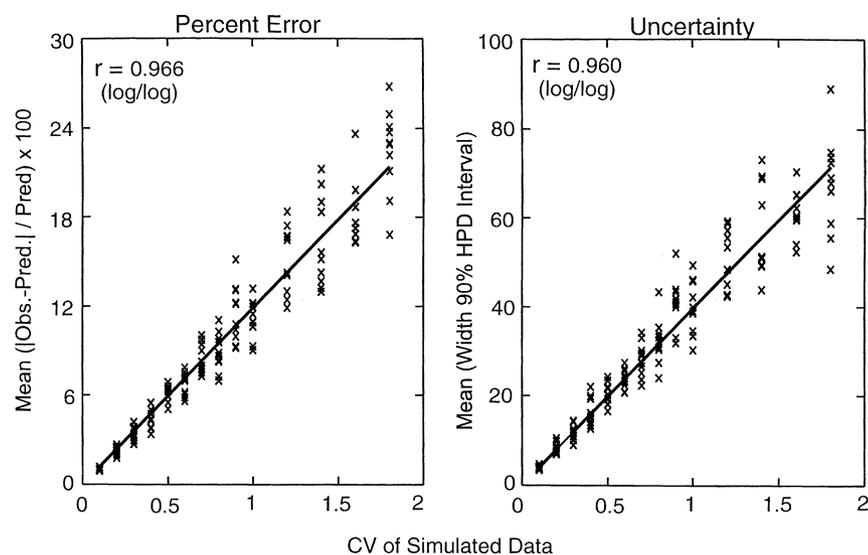


Figure 4 Relationship between time series variability, prediction accuracy, and prediction uncertainty for simulated data with different coefficients of variation (CVs). Mean values for each simulation are indicated with an “X”; the line shows a simple linear regression with no intercept through the data.

postmanipulation; Findlay & Kling 1975; Leavitt & Findlay 1994) and which are known to increase during lake eutrophication elsewhere (e.g. Harper 1992; Cottingham *et al.* 1998).

Our analyses also support the hypothesis that ecosystem variability increases, while predictability declines, with enrichment, although the variability analyses were sensitive to the precise pigment used to estimate total algal abundance. For example, time series variability increased and predictability declined for the labile, ubiquitous pigment chlorophyll *a* and the sum of biomarker pigments, but not for the equally widespread, stable β -carotene (Figs 2, 3). We infer that this pattern may reflect changes in the relative proportion of benthic and planktonic algae resulting from eutrophication, as detailed in Leavitt *et al.* (1994). As shown elsewhere, fertilization of chrysophyte-rich lakes leads to a loss of chrysophyte blooms (Cottingham *et al.* 1998), the main source of undegraded chlorophyll *a* to sediments (Leavitt 1993). In contrast, sedimentary β -carotene arises equally from both benthic and planktonic sources (Leavitt *et al.* 1999). Given that increased variability was observed mainly for pigments representing planktonic cryptophytes, chlorophytes and N_2 -fixing cyanobacteria, and not algae with substantial benthic sources (e.g. fucoxanthin from diatoms), our results suggest that increased variability following fertilisation is a planktonic phenomenon in lakes. This contrasts with results from marine communities that show a significant response of benthic communities to pollutants (Warwick *et al.* 1990; Agard *et al.* 1993). However, given the complex biogeochemistry of sedimentary pigments (Leavitt 1993), further research is required to verify this hypothesis.

DLMs fit to simulated data revealed that time series predictability should decline whenever variability in-

creases (Fig. 4). This pattern was especially well developed for our empirical analyses of N_2 -fixing cyanobacteria, consistent with observed difficulties in forecasting cyanobacterial blooms in other strongly stratified eutrophic lakes (Klemer & Konopka 1989; Soranno 1997). Because plankton form a higher proportion of total primary production in eutrophic lakes than in less fertile systems (Björk-Ramberg 1983), there exists the possibility that transmission of variance throughout aquatic food webs may also destabilise upper trophic levels in eutrophic ecosystems (e.g. Kitchell 1992). In addition, our analysis reinforces the observation that DLM performance is strongly influenced by the characteristics of variability in the underlying time series (Cottingham & Carpenter 1998).

Consequences of increased community and ecosystem variability

Increased community and ecosystem variability may be a widespread consequence of human activities that obscures impacts of long-term global change, diminishes biodiversity, and reduces the effectiveness of scientific experiments and management strategies. For example, intense human activities have already increased both N and P flux to many terrestrial and aquatic ecosystems (Vitousek *et al.* 1997; Carpenter *et al.* 1998). If fertilisation increases inherent community and ecosystem variability, then it may increase the length of time required before impacts of climate change (e.g. Hulme *et al.* 1999) and other interacting stressors (Breitburg *et al.* 1999) can be distinguished from background variance. Similarly, because the rate of loss of rare species can be greater for variable than stable ecosystems (Pimm *et al.* 1988),

eutrophication may confound investigations of biodiversity–stability relationships (see Tilman 1999). In both cases, delays in effective management are likely to result, with profound economic and biological impacts (e.g. Reilly *et al.* 1999).

Increased variability due to fertilisation may also reduce the effectiveness of critical ecosystem experiments and environmental monitoring. Because the assumption of constant variance will not be met, sensitivity of analyses based on intersite comparisons (e.g. Before–After–Control–Impact designs, Underwood 1991; randomized intervention analysis, Carpenter *et al.* 1989) will decline. This problem will be particularly acute if the designs are not balanced (Glasby 1997).

In conclusion, we have used annual palaeoecological records from a manipulated lake to demonstrate that fertilisation increased the variability and reduced the predictability of algal community and ecosystem variables. Our analyses suggest that this phenomenon is not an artefact of statistical changes in mean abundance, but rather may be an inherent feature of eutrophic ecosystems. Further, our simulations suggest that declines in the accuracy of forecasts from time series data will be a statistical inevitability whenever variability increases. Finally, while provocative, we hypothesise that such increases in community and ecosystem variability may be widespread, arising from pervasive human supplements to natural biogeochemical cycles.

ACKNOWLEDGEMENTS

The authors thank Keith Somers, Bryan Manly, Bruce Kendall, Fiorenza Micheli, and Eric Seabloom for advice on statistical analyses; Dave Findlay and Marianne Douglas for coring assistance; Alistair Hardie for HPLC analyses; and Bryan Brown, Jay Lennon, Michel Loreau and two anonymous reviewers for comments on previous drafts of this manuscript. KLC was supported by the National Center for Ecological Analysis and Synthesis (a centre jointly funded by the U.S. National Science Foundation, the State of California, and the University of California at Santa Barbara) and Dartmouth College. JAR was supported by an NSERC Postgraduate Scholarship and NSERC Research Grants to Norman Yan, Donald McQueen and PRL. PRL was supported by an NSERC Research Grant.

REFERENCES

- Abrams, P.A. & Walters, C.J. (1996). Invulnerable prey and the paradox of enrichment. *Ecology*, *77*, 1125–1133.
- Agard, J.B.R., Gobin, J. & Warwick, R.M. (1993). Analysis of marine macrobenthic community structure in relation to pollution, natural oil seepage and seasonal disturbance in a tropical environment (Trinidad, West Indies). *Mar. Ecol. Prog. Series*, *92*, 233–243.
- Björk-Ramberg, S. (1983). Production of epipelagic algae before and during lake fertilization in a subarctic lake. *Holarctic Ecol.*, *6*, 349–355.
- Breitburg, D., Seitzinger, S. & Sanders, J., eds. (1999). The effects of multiple stressors on freshwater and marine ecosystems. *Limnol. Oceanogr.*, *44*, 739–972.
- Carpenter, S.R., Frost, T.M., Heisey, D. & Kratz, T.K. (1989). Randomized intervention analysis and the interpretation of whole-ecosystem experiments. *Ecology*, *70*, 1142–1152.
- Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N. & Smith, V.H. (1998). Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Applications*, *8*, 559–568.
- Cottingham, K.L. & Carpenter, S.R. (1998). Population, community, and ecosystem variates as ecological indicators: phytoplankton responses to whole-lake enrichment. *Ecol. Applications*, *8*, 508–530.
- Cottingham, K.L., Carpenter, S.R. & St. Amand, A.L. (1998). Responses of epilimnetic phytoplankton to experimental nutrient enrichment in three small seepage lakes. *J. Plankton Research*, *20*, 1889–1914.
- Findlay, D.L. & Kling, H.J. (1975). Seasonal successions of phytoplankton in seven lake basins in the experimental lakes area Northwestern Ontario following artificial eutrophication. *Can. Fish. Mar. Serv. Technical Report*, 513.
- Glasby, T.M. (1997). Analysing data from post-impact studies using asymmetrical analyses of variance: a case study of epibiota on marinas. *Aust. J. Ecology*, *22*, 448–459.
- Harper, D. (1992). *Eutrophication of Freshwaters*. Chapman & Hall, New York, NY, USA.
- Hulme, M., Barrow, E.M., Arnell, N.W., Harrison, P.A., Johns, T.C. & Downing, T.E. (1999). Relative impacts of human-induced climate change and natural climate variability. *Nature*, *397*, 688–691.
- Keyes, T.K. & Levy, M.S. (1997). Analysis of Levene's test under design imbalance. *J. Educational Behav. Statistics*, *22*, 227–236.
- Kitchell, J.F. (1992). *Food Web Management*. Springer Verlag, New York.
- Klemer, A.R. & Konopka, A.E. (1989). Causes and consequences of blue-green algal (cyanobacterial) blooms. *Lake Reservoir Management*, *5*, 9–19.
- Lamon, E.C. III, Carpenter, S.R. & Stow, C.A. (1998). Forecasting PCB concentrations in Lake Michigan salmonids: a dynamic linear model approach. *Ecol. Applications*, *8*, 659–668.
- Leavitt, P.R. (1993). A review of factors that regulate carotenoid and chlorophyll deposition and fossil pigment abundance. *J. Paleolimnol.*, *9*, 109–127.
- Leavitt, P.R. & Findlay, D.L. (1994). Comparison of fossil pigments with 20 years of phytoplankton data from eutrophic Lake 227, Experimental Lakes Area, Ontario. *Can. J. Fish Aquat. Sci.*, *51*, 2286–2299.
- Leavitt, P.R., Hann, B.J., Smol, J.P., Zeeb, B.A., Christie, C.E., Wolfe, B. & Kling, H.J. (1994). Paleolimnological analysis of whole-lake experiments: an overview of results from Experimental Lakes Area Lake 227. *Can. J. Fish Aquat. Sci.*, *51*, 2322–2332.
- Leavitt, P.R., Findlay, D.L., Hall, R.I. & Smol, J.P. (1999). Algal responses to dissolved organic carbon loss and pH decline during whole-lake acidification: Evidence from paleolimnology. *Limnol. Oceanogr.*, *44*, 757–773.

- Murdoch, W.W., Nisbet, R.M., McCauley, E., deRoos, A.M. & Gurney, W.S.C. (1998). Plankton abundance and dynamics across nutrient levels: tests of hypotheses. *Ecology*, 79, 1339–1356.
- Odum, E.P., Finn, J.T. & Franz, E.H. (1979). Perturbation theory and the subsidy-stress gradient. *Bioscience*, 29, 349–352.
- Pimm, S.L., Jones, H.L. & Diamond, J. (1988). On the risk of extinction. *Am. Naturalist*, 132, 757–785.
- Reilly, J., Harnisch, J., Fitzmaurice, J., Jacoby, H., Kicklighter, D., Melillo, J., Stone, P. & Wang, C. (1999). Multi-gas assessment of the Kyoto Protocol. *Nature*, 401, 549–555.
- Rosenzweig, M.L. (1971). Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, 171, 385–387.
- Scheffer, M. & De Boer, R.J. (1995). Implications of spatial heterogeneity for the paradox of enrichment. *Ecology*, 76, 2270–2277.
- Schindler, D.W. (1988). Experimental studies of chemical stressors on whole lake ecosystems. *Verhandlungen Internationale Vereinigung Limnologie*, 23, 11–41.
- Schultz, B.B. (1985). Levene's test for relative variation. *Syst. Zool.*, 34, 449–456.
- Soranno, P.A. (1997). Factors affecting the timing of surface and epilimnetic blooms of blue-green algae in a eutrophic lake. *Can. J. Fish Aquat. Sci.*, 54, 1965–1975.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80, 1455–1474.
- Underwood, A.J. (1991). Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Aust. J. Mar. Freshwater Res.*, 42, 569–587.
- Underwood, A.J. (1997). *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge, UK.
- Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. & Tilman, D.G. (1997). Human alteration of the global nitrogen cycle: Sources and consequences. *Ecol. Applications*, 7, 737–750.
- Warwick, R.M. & Clarke, K.R. (1993). Increased variability as a symptom of stress in marine communities. *J. Exp. Mar. Biol. Ecol.*, 172, 215–226.
- Warwick, R.M., Platt, H.M., Clarke, K.R., Agard, J. & Gobin, J. (1990). Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. *J. Exp. Mar. Biol. Ecol.*, 138, 119–142.
- West, M. & Harrison, J. (1997). *Bayesian Forecasting and Dynamic Models*. 2nd edn. Springer-Verlag, New York, NY, USA.
- Yodzis, P. & Innis, S. (1992). Body size and consumer-resource dynamics. *Am. Naturalist*, 139, 1151–1175.

BIOSKETCH

Kathryn L. Cottingham is a quantitative ecologist interested in the temporal dynamics of complex communities, especially freshwater lakes and ponds. Her current research projects seek to (a) develop a predictive understanding of community responses to perturbation and (b) understand relationships between variability in community composition and in ecosystem processes.

Editor, M. Loreau

Manuscript received 3 April 2000

Manuscript accepted 12 April 2000