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# Fingerprints of biocomplexity: Taxon-specific growth of phytoplankton in relation to environmental factors

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*Abstract*

Phytoplankton and environmental conditions in Lake Washington, Seattle, Washington, are discussed from the perspective of dynamic relationships between taxon-specific growth rates and environmental variables. More than four decades of measurements permit inspection of conditions associated with net increase and decrease for 40 phytoplankton species or species groups. Reproducible patterns exist for growth responses to over 25 environmental factors including nutrient chemistry, physical variables, and herbivorous zooplankton species. There appear to be no more than six main modalities of response to environmental factors, and responses to chemical and physical variables show coherence across taxa. Diatoms show a near uniform positive growth response to abundant inorganic nutrients, cold and transparent water, deep mixing, and intolerance for virtually all zooplankton grazers. Many chlorophytes and cyanobacteria show equally uniform growth responses to chemical and physical variables, although their preferences are virtually opposite from the diatoms. They benefit from the presence of copepods but show highly specific growth rate responses to different cladocerans and rotifers. Growth rate variations among the diatoms sort out along gradients of resource and physical factors, but there is coherence to the rise and fall of multiple species. Among the other algal divisions, despite a common set of physical and chemical conditions that promote growth rates, the species do not increase and decrease together. Instead, the prevailing grazer community appears to shape the phytoplankton community by admitting only certain species from the large pool of contenders.

The idea of using distributions and dynamics of organisms to deduce evolutionary adaptive strategies that allow species to propagate and prosper has proved illuminating for both terrestrial plant and phytoplankton ecologists (Margalef 1978; Grime 1979; Reynolds 1988). Strategies have been defined as traits that permit a taxon or group of taxa to become better suited to particular sets of environmental conditions. Both Grime and Reynolds have argued that various strategies have tended to sort out along three major axes or lines of adaptive specialization. They identify ''stress,'' ''disturbance,'' and ''competition'' as the key themes that shape plant communities by natural selection.

When we inspect natural communities, however, there is a challenge in attempting to reconcile these concepts (e.g., stress) with specific environmental measurements. Stress, disturbance, and competition are abstractions of natural phenomena, and hence they have no objective existence that is mandatory for unambiguous, reproducible measurement. This is not meant to decry the value of metaphor in systems as complex as biological communities, but it does suggest the need for approaches to adaptive strategies that link tightly with environmental data. Open water communities of planktonic algae have commanded scrutiny ever since G. E. Hutchinson articulated the ''paradox of the plankton'' to highlight the existence of profound biodiversity within a superficially homogeneous medium. Reconciliation of the paradox requires demonstration of the true complexity that exists within that world, and strict demonstration calls for more than analogy and metaphor.

Few data sets permit detailed inspection of the complex interrelationships among phytoplankton dynamics, water chemistry, lake physics, and herbivore communities over decadal time scales, but Lake Washington at Seattle offers such opportunity. Long-term changes in the phytoplankton community of that lake during the second half of the 20th century have recently been described (Edmondson et al. 2003), along with an introduction to associated physical and chemical variables. The report by Edmondson et al. focused on interannual variations and on the major phytoplankton transitions that accompanied alterations in nutrient income and herbivore community.

We here turn our attention from describing the long-term community transformations to inquiries about the mechanistic basis for species success, decline, and community transitions. The time period for this study spans 5 decades and encompasses dramatic episodes of cultural eutrophication and recovery, as well as progressive land development, watershed management, and manipulation of fish communities. Previous work has divided the long interval into three major eras: eutrophication (1941–1968), recovery (1969–1975), and *Daphnia* era (1976–present). In this study we will re-

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*Acknowledgments*

W. Thomas Edmondson passed away 10 January 2000 after we had started the work on this paper. The long record of data on Lake Washington comes from the work of many colleagues: technicians, students, postdoctoral associates, and volunteers. The most directly involved included Katie P. Frevert, the late David E. Allison, and the late Mardi I. Varela. The work was supported by a series of grants from the U.S. National Science Foundation and by the Andrew W. Mellon Foundation.

focus from the temporal mesoscale (seasons to years) to examine the growth patterns and associated environmental variables at week to week scale throughout the entire period of record.

Approximately 40 phytoplankton taxa have been characterized as key elements in the changing lake community of Lake Washington (Edmondson et al. 2003). The aim of this paper is to examine the environmental conditions that exist during times of net positive growth (increase) as well as net negative growth (decrease) for the key taxa individually and for various aggregated groups. This approach permits recognition of consistent patterns as well as formulation of hypotheses about differential roles of physical, nutrient chemical, and grazer control factors in the rise and fall of individual or allied taxa.

## Methods

*Description and reconciliation of the time series data*—The first step in this analysis was to construct a common time basis for intercomparison of diverse data types. The specific methods used to collect and measure each variable are described by Edmondson et al. (2003). Observations of weather conditions, lake physics, water chemistry, phytoplankton biovolume, crustaceans, and rotifers were not always simultaneous.

Lake chemistry data for the surface mixed layer (TP [total P after perchlorate oxidation], DP [filterable P after perchlorate oxidation], SRP [soluble reactive P], raw $PO_4$-P [unfiltered molybdate reactive $PO_4$-P], $\Sigma$N [total Kjeldahl N: $NH_3$-N + organic N], $NO_3$-N, $NO_2$-N, $NH_3$-N, SRSi [soluble reactive Si], ANC [acid neutralizing capacity, or titration alkalinity], and pH) were treated as contemporaneous if they were measured within 24 h of each other. Replicate values obtained on a single date were averaged.

Observations of Secchi transparency depth, mean temperature of the surface mixed layer ($T_{mix}$), and depth of the mixed layer ($Z_{mix}$) were treated as contemporaneous if the dates were within 24 h of each other. Additional estimates for Secchi depth needed to correspond with $T_{mix}$ and $Z_{mix}$ were obtained by linear interpolation. These supplemental derived values were combined with the primary data and initially tracked as a separate (derived) variable: $SD_{interp}$. Daily records for insolation and wind speed were averaged for the dates between $T_{mix}$ and $Z_{mix}$ sample dates. The resulting variables Mean $I_0$ and Mean Wind thus represented mean values over a sampling interval. An index variable for mean light intensity in the mixed layer was derived as

$$I_{mean} = \text{Mean } I_0/(Z_{mix}/SD_{interp}) \quad (1)$$

Zooplankton abundances were expressed as animals per cubic meter and were arrayed on a common time grid using the same criteria for contemporaneous values as were applied to the chemistry and physical variables and averaging. Biovolume estimates for phytoplankton taxa were expressed as $mm^3\ L^{-1}$.

The sampling interval varied seasonally and to some degree across the years. Sampling was typically weekly from March to October and biweekly or occasionally triweekly at other times. However, in some years the weekly regime was maintained for the full year. From 1962 to 1997, the mean sampling interval was 11.1 d (SD = 5.2 d).

*Growth phase characterization*—A protocol implemented in Microsoft Excel™ was developed to identify periods of sustained increase or decrease in algal taxon groups:

1. Dates were flagged positive (POSflag) if they were part of a series of at least four consecutive monotonically increasing values of biovolume for the specified taxon.
2. Dates were flagged negative (NEGflag) if they were part of a series of at least four consecutive monotonically decreasing values of biovolume for the specified taxon.
3. Neither endpoint of the monotonic biovolume series was counted in either the POSflag or NEGflag series.
4. POSflag and NEGflag date masks developed from taxon-specific phytoplankton biomass (binary flags: 0 or 1) were used to identify environmental variables on the associated dates.
5. POSflag and NEGflag date masks were used to extract the full set of environmental variables associated with positive or negative growth intervals, as defined in steps 1 and 2.
6. Summary statistics and comparisons were performed on the extracted data in order to compare the attributes of environmental variables during times of positive and negative net growth rates that were taxon specific.

The adopted protocol represented a conservative way to identify periods of sustained increase and to segregate them from periods of sustained decrease. Our reasoning was that isolated jumps or drops in biovolume from one sampling date to the next could arise from many causes including artifacts, and it could not be certain whether the environmental conditions at each such date were associated with positive, negative, or indeterminate population growth. If a net growth trajectory was maintained across at least four sample dates, however, we considered it justifiable to regard the environmental conditions during the core dates of the interval (e.g., dates two and three for a four-date monotonic series) as being indicative of conditions permissive of net increase or net decrease.

Prior to statistical comparisons, the environmental variables including zooplankton abundances were subjected to inspection and statistical test for symmetry and normality. Transformations were applied to the variables to permit application of parametric statistical tests whenever appropriate. In order to permit logarithmic transformation in cases when analytical results yielded chemical concentrations that were indistinguishable from blank (zero concentration), the ''zero'' values were adjusted to the approximate minimum values of analytical detection as reported in the data set. The adjustment values and numbers of cases affected were as follows:

| | | |
|---|---|---|
| DP: | $+1.0\ \mu g\ L^{-1}$ | (6 cases out of 758) |
| SRP: | $+0.2\ \mu g\ L^{-1}$ | (55 cases out of 852) |
| raw $PO_4$-P: | $+0.2\ \mu g\ L^{-1}$ | (89 cases out of 1,038) |
| $NO_3$-N: | $+2\ \mu g\ L^{-1}$ | (28 cases out of 957) |
| $NO_2$-N: | $+0.1\ \mu g\ L^{-1}$ | (126 cases out of 392) |
| $NH_3$-N: | $+0.2\ \mu g\ L^{-1}$ | (72 cases out of 370) |

Table 1. Descriptive statistics for the environmental variables used to test for differences between positive net growth and negative net growth by different phytoplankton taxa. Variable names that begin with ''LN'' indicate that the native data were transformed by natural logarithm. Unless indicated otherwise, water chemistry variable units are $\mu$g $L^{-1}$ before transformation. Insolation (Mean $I_0$ and $I_{mean}$) are in g-cal $cm^{-2}$ $d^{-1}$; wind speed is m $s^{-1}$. Chemistry data range from 14 Jan 1933 to 24 Mar 1999. Physical data range from 7 Jan 1950 to 24 Mar 1999.

| Variable name | Mean | Median | SD | *n* | Min | Max |
|---|---|---|---|---|---|---|
| LN(TP) | 2.85 | 2.82 | 0.64 | 874 | 0.69 | 4.63 |
| LN(DP) | 2.13 | 1.97 | 0.80 | 758 | 0.00 | 4.36 |
| LN(raw $PO_4$-P) | 1.17 | 0.99 | 1.54 | 1,038 | −1.61 | 4.13 |
| LN(SRP) | 1.00 | 0.77 | 1.48 | 852 | −1.61 | 4.08 |
| SRSi (mg $L^{-1}$) | 1.62 | 1.58 | 0.805 | 475 | 0.01 | 3.46 |
| LN($\Sigma$N) | 5.68 | 5.62 | 0.42 | 438 | 3.74 | 6.98 |
| LN($NO_3$-N) | 4.38 | 4.80 | 1.39 | 957 | 0.69 | 6.30 |
| LN($NO_2$-N) | −0.82 | −0.92 | 1.37 | 392 | −2.30 | 3.43 |
| LN($NH_3$-N) | 1.58 | 2.17 | 1.80 | 370 | −1.61 | 5.16 |
| ANC (mEq) | 0.68 | 0.68 | 0.082 | 957 | 0.28 | 0.82 |
| PH | 7.96 | 7.80 | 0.625 | 982 | 6.3 | 9.95 |
| Secchi (m) | 5.0 | 5 | 2.2 | 1,993 | 0.7 | 12.9 |
| $SD_{interp}$ (m) | 4.9 | 4.8 | 2.2 | 2,146 | 0.7 | 12.9 |
| $Z_{mix}$ (m) | 26.5 | 14 | 23.6 | 1,655 | 1 | 65 |
| $T_{mix}$ (m) | 13.4 | 13.3 | 5.1 | 1,655 | 4.2 | 23.8 |
| Mean $I_0$ | 309.6 | 309.4 | 172.8 | 2,059 | 29.6 | 755.6 |
| Mean wind | 8.1 | 8.1 | 1.7 | 2,001 | 1.4 | 14.42 |
| $I_{mean}$ | 140.6 | 73.7 | 192.9 | 1,574 | 1.6 | 2,410.4 |

Table 2. Descriptive statistics for the natural logarithm transformations of nonzero zooplankton abundances (animals $m^{-3}$) by taxon and life stage. Abundance data range from 11 Feb 1950 to 30 Nov 1998. Dg = *Daphnia galeata*; Dt = *Daphnia thorata.*

| Ln-transformed | Mean | Median | SD | *n* | Min | Max |
|---|---|---|---|---|---|---|
| *Diaptomus* C6 | 7.58 | 7.67 | 1.10 | 1,307 | 0 | 10.35 |
| *Diaptomus* C1–C6 | 9.14 | 9.11 | 1.16 | 1,316 | 3.33 | 12.25 |
| *Epischura* C6 | 4.12 | 4.29 | 1.72 | 1,200 | 0 | 8.37 |
| *Epischura* C1–C6 | 5.38 | 5.53 | 1.72 | 1,269 | 0 | 9.08 |
| cyclopoids C1–C6 | 8.89 | 8.91 | 0.94 | 1,315 | 3.91 | 11.66 |
| *Diaphanosoma* | 5.34 | 5.32 | 2.30 | 842 | 0.69 | 10.24 |
| *Bosmina* | 5.56 | 5.58 | 1.95 | 1,088 | 0.69 | 10.99 |
| *Daphnia* adults | 5.81 | 6.44 | 2.35 | 797 | 0 | 9.58 |
| *Daphnia* total | 6.75 | 7.54 | 2.64 | 890 | 0 | 10.89 |
| *D. pulicaria* adults | 5.45 | 6.00 | 2.29 | 719 | 0 | 9.55 |
| *D. pulicaria* total | 6.46 | 6.97 | 2.51 | 772 | 0.47 | 10.84 |
| Dg + Dt adults | 5.06 | 5.28 | 1.99 | 598 | 0.41 | 9.27 |
| Dg + Dt total | 5.86 | 6.18 | 2.36 | 661 | 0.47 | 10.29 |
| *Conochilus unicornis* | 7.11 | 6.91 | 2.32 | 467 | 2.30 | 12.73 |
| *Conochilus hippocrepis* | 7.94 | 7.78 | 2.17 | 310 | 1.61 | 13.71 |
| *Keratella quadrata* | 5.53 | 5.43 | 1.48 | 357 | 2.20 | 10.76 |
| *Keratella cochlearis* | 7.57 | 7.29 | 2.31 | 995 | 2.48 | 14.69 |
| *Kellicottia longispina* | 7.84 | 7.88 | 1.79 | 1,113 | 2.56 | 13.53 |
| *Notholca* | 5.23 | 5.23 | 1.18 | 76 | 3.00 | 7.85 |
| *Polyarthra* | 7.70 | 7.68 | 2.00 | 949 | 2.48 | 13.28 |
| *Ascomorpha* | 5.44 | 5.24 | 1.42 | 135 | 2.30 | 9.65 |
| *Trichocerca* | 5.94 | 5.76 | 1.91 | 280 | 2.20 | 13.21 |
| *Ploesoma* | 5.31 | 5.36 | 1.19 | 36 | 3.30 | 8.67 |
| *Filinia* | 5.62 | 5.62 | 1.53 | 107 | 2.77 | 9.99 |
| *Synchaeta pectinata* | 6.25 | 6.09 | 1.77 | 240 | 2.08 | 10.86 |
| Other *Synchaeta* | 6.18 | 6.13 | 1.74 | 358 | 2.30 | 11.34 |

In order to ascertain the number of orthogonal axes (independent variables) represented in fact by the data sets, each data set (chemistry, physics, zooplankton) was subjected to principal components analysis (Systat 5.01) weighting the variables according to their correlations.

## Results

*Transformation of variables*—Most of the environmental variables exhibited skew characteristic of lognormal distributions (e.g., serious departure of mean/median ratios from 1.0) that could be largely corrected by logarithmic transformation. Table 1 lists descriptive statistics for the global set of chemical and physical variables that was ultimately used in this study. Transformation was applied to all water chemistry variables except pH, ANC, and SRSi. Physical variables appeared suitable for use without transformation, with two exceptions. Both $Z_{mix}$ and $I_{mean}$ (derived from $Z_{mix}$) have bimodal distributions, and hence neither one can be transformed to approximate a symmetrical Gaussian shape. Statistics applied to these variables must therefore be interpreted with due caution.

Zooplankton frequency distributions were all strongly lognormal. Transformation by natural logarithm produced symmetrical unimodal distributions (Table 2).

Principal components analyses (PCA) revealed that five independent axes are required to represent 95% of the variance within the chemistry data set. Five independent axes were needed to account for 95% of the variance in the physical variables, as well. Orthogonal transformation of the variable axes was not conducted, however. Variables were contemporaneous (all variable measurements available simultaneously) on only 1,353 of 2,136 dates for physical variables and on only 271 of 1,249 dates for chemical var-

Table 3. Descriptive statistics for the natural logarithm transformations of nonzero algal biovolume ($mm^3\ L^{-1}$) by taxon. Data time period ranges from 11 Feb 1950 to 22 Dec 1997. See Edmondson et al. (2003) table 3 for more detail about the taxa included in aggregated categories.

| Ln-transformed | ID | Mean | Median | SD | *n* | Min | Max |
|---|---|---|---|---|---|---|---|
| *Oocystis gigas* | G1 | −3.35 | −3.38 | 1.52 | 339 | −6.90 | 0.24 |
| Other *Oocystis* spp. | G2 | −6.22 | −6.15 | 1.32 | 465 | −11.11 | −2.41 |
| *Staurastrum paradoxum* | G3 | −4.89 | −4.84 | 1.13 | 195 | −7.03 | −1.50 |
| Gelatinous greens | G4 | −5.85 | −5.72 | 1.54 | 722 | −10.41 | −2.11 |
| Acicular greens | G5 | −6.78 | −6.65 | 1.39 | 921 | −11.87 | −1.71 |
| *Botryococcus* spp. | G6 | −3.78 | −3.69 | 1.73 | 57 | −7.75 | −0.91 |
| Other greens | G7 | −5.92 | −5.79 | 1.39 | 762 | −10.48 | −2.85 |
| *Asterionella formosa* | D8 | −4.44 | −4.47 | 1.74 | 729 | −8.77 | 1.73 |
| *Cyclotella pseudostelligera* | D9 | −7.52 | −7.72 | 1.69 | 411 | −11.18 | −1.67 |
| *C. bodanica* + *C. comta* | D10 | −4.74 | −4.76 | 1.40 | 146 | −8.52 | −0.69 |
| *C. ocellata* | D11 | −5.99 | −6.03 | 1.46 | 289 | −10.01 | −1.51 |
| *Diatoma elongatum* | D12 | −3.19 | −3.59 | 2.60 | 61 | −9.21 | 1.17 |
| *Fragilaria crotonensis* | D13 | −3.92 | −3.95 | 2.05 | 890 | −9.57 | 1.45 |
| *Aulacoseira subarctica* | D14 | −3.11 | −3.09 | 1.89 | 868 | −9.50 | 0.80 |
| *Aulacoseira italica* v. *tenuissima* | D15 | −4.98 | −4.99 | 1.56 | 563 | −8.87 | −0.59 |
| *Melosira varians* | D16 | −4.50 | −4.37 | 1.30 | 131 | −7.80 | −0.74 |
| *Rhizosolenia eriensis* | D17 | −5.65 | −5.83 | 1.67 | 315 | −9.61 | 0.83 |
| *Steph. neoastraea* + *S. minutula* | D18 | −4.35 | −4.44 | 1.81 | 526 | −8.91 | 0.33 |
| *Steph. hantzschii* + *S. alpinus* | D19 | −5.84 | −6.20 | 1.73 | 297 | −10.01 | −0.66 |
| *Steph. niagarae* | D20 | −1.33 | −1.44 | 1.56 | 412 | −6.36 | 2.64 |
| Large *Synedra* spp. | D21 | −5.45 | −5.57 | 1.77 | 782 | −10.52 | −0.51 |
| *Synedra tenera* | D22 | −5.91 | −6.02 | 1.67 | 243 | −9.16 | −1.55 |
| *Tabellaria fenestrata* | D23 | −2.89 | −2.92 | 1.98 | 270 | −7.12 | 1.74 |
| Other diatoms | D24 | −6.18 | −6.22 | 1.82 | 968 | −11.11 | 0.21 |
| *Mallomonas* spp. | M25 | −5.88 | −5.98 | 1.34 | 375 | −10.18 | −1.80 |
| *Chroomonas minuta* | C26 | −4.72 | −4.52 | 1.30 | 1,112 | −9.17 | −0.86 |
| *Cryptomonas* | C27 | −3.42 | −3.39 | 1.38 | 1,109 | −8.06 | 0.32 |
| *Anabaena* | B28 | −4.96 | −5.20 | 2.18 | 694 | −10.68 | 2.12 |
| *Aphanizomenon* | B29 | −5.11 | −5.07 | 1.91 | 613 | −9.76 | 0.18 |
| *Chroococcus limneticus* | B30 | −5.48 | −5.51 | 1.38 | 237 | −8.92 | −0.82 |
| *Coelosphaerium* | B31 | −5.59 | −5.60 | 1.73 | 391 | −12.72 | 0.53 |
| *Microcystis* | B32 | −5.97 | −6.11 | 1.90 | 183 | −9.40 | 0.22 |
| *Lyngbya limnetica* | B33 | −5.04 | −4.93 | 2.30 | 511 | −13.12 | 0.94 |
| *Oscillatoria* | B34 | −1.33 | −1.09 | 2.07 | 466 | −9.63 | 2.54 |
| *Pseudanabaena* | B35 | −4.57 | −4.83 | 1.48 | 46 | −7.78 | −1.10 |
| *Schizothrix* | B36B | −4.04 | −4.09 | 2.24 | 273 | −9.88 | 1.11 |
| Other colonial coccoid bluegreens | B37 | −6.70 | −6.64 | 1.80 | 482 | −11.51 | −1.28 |
| Other bluegreens | B38 | −6.94 | −7.06 | 2.41 | 289 | −12.43 | −0.82 |
| *Ceratium hirundinella* | F39 | −2.42 | −2.24 | 1.16 | 55 | −5.93 | −0.53 |
| Other dinoflagellates | F40 | −5.61 | −5.59 | 1.28 | 311 | −9.53 | −2.13 |
| All others | O41 | −3.20 | −3.19 | 0.86 | 1,248 | −7.82 | −0.41 |
| Total (1–41) | T42 | 0.40 | 0.33 | 1.13 | 1,252 | −2.37 | 3.56 |

iables. The reduction in power and resolution that would result from a transformation of the coordinates was deemed not worthwhile. It was easy to understand that there were high correlations among several of the variables and that the results could be interpreted by considering them as a suite. For example, 57% of the overall variance in the water chemistry data could be assigned to a single axis that was dominantly constructed of SRP, DP, raw $PO_4$-P, $NO_3$-N, and SRSi (positive correlations) plus ANC (negative correlation). The second major component of variance (20% of total) was dominated by $\Sigma N$ and $NH_3$ (positive correlations). The third element (12% of total variance) was dominated by TP (negative loading) and $NO_2$ (positive). These results elucidate the somewhat obvious large-scale features of a data set that contains data from eutrophic years as well as from unenriched conditions.

Zooplankton abundances by taxon also exhibit correlations. Principal components analysis applied to the zooplankton data revealed that 12 orthogonal axes are required to account for 95% of the variance in the data. There was some obvious redundancy in the data set stemming from nested variable categories. For example, adult *Diaptomus* and adult *Epischura* correlate necessarily with total copepodids of each taxon ($r = 0.637$ and 0.799, respectively). Abundance of adult *Daphnia* correlates tightly with total abundance of *Daphnia* ($r = 0.965$), adult *Daphnia pulicaria* ($r = 0.928$), total *D. pulicaria* ($r = 0.881$), and total *D. galeata* plus *D. thorata* ($r = 0.817$).

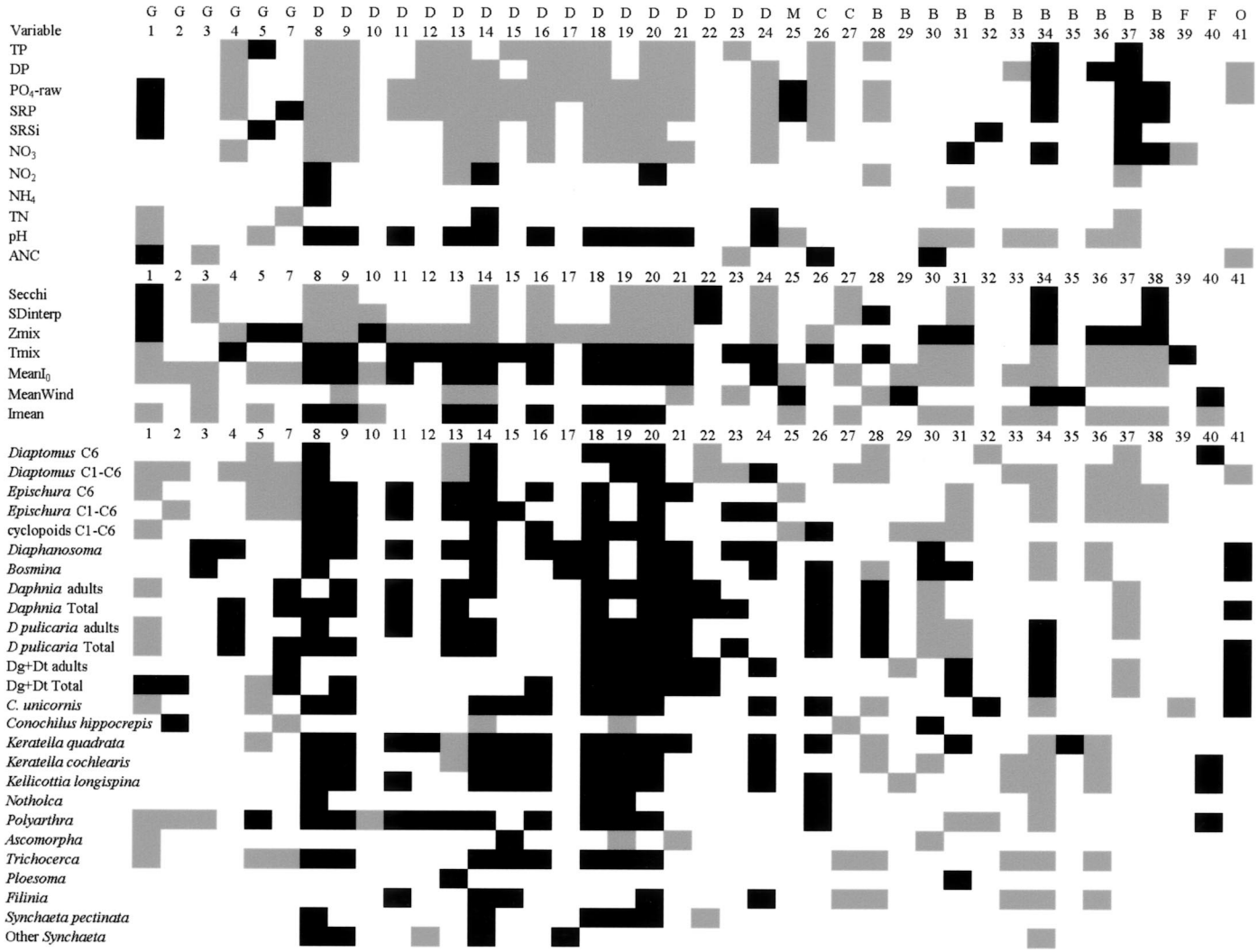


Fig. 1. Net growth relationships between individual algal taxa and environmental variables. Gray denotes that the net positive growth is associated with statistically higher values of the environmental variable (positive relationship between variable and growth rate). Black denotes that net negative growth is associated with statistically higher values of the variable (negative relationship). White indicates that no consistent, statistically significant relationship could be established between growth rate and the variable.

The results from PCA were used as a guide for the numbers of independent variables that could realistically be inspected for effects on algal growth rates. Table 3 lists the algal taxa that were investigated. The longevity of the Lake Washington data set has the disadvantage that taxonomic revisions have affected many of the species studied over time, for example some of the bluegreen algae (Anagnostidis and Komárek 1988). Nonetheless, for consistency of reporting and for comparison with our previous publications, we have retained the older names in this paper. For each taxon, environmental variables (Tables 1 and 2) extracted during times of net positive growth and net negative growth were compared by two-tail *t*-test to ascertain whether the two subsets differed in mean value. If the mean values differed at $\alpha = 0.05$, the variable was flagged to differentiate whether the value of the environmental variable was greater during times of net positive growth or net negative growth.

Figure 1 illustrates the resulting environmental ''fingerprints'' from the statistical tests by taxon. Because of the high correlations and consistency of responses among all measured forms of phosphorus, a composite variable P vars was defined to represent the collective responses to TP, DP, SRP, and raw $PO_4$-P. Because of consistency of response across taxa, $NH_3$ and $NO_2$ were combined with $\Sigma N$. This reduced the number of water chemistry variables to six, which is close to the five orthogonal axes identified by PCA. Further consolidation would have been possible by combining silica or nitrate with phosphorus, but we decided to retain the identification of these different elements.

The physical variable set was reduced to five by discarding Secchi in favor of the supplemented data series $SD_{interp}$, and we aggregated $T_{mix}$ and Mean $I_0$ as ''heat vars.''

The zooplankton variable set was reduced to 13 by first aggregating the two *Diaptomus* categories as ''*Diaptomus*,'' and the two *Epischura* categories as ''*Epischura*.'' Then, five highly correlated *Daphnia* categories were aggregated as

Table 4. Environmental variables, including aggregate variables, and the number of taxon-specific cases for each when positive net growth rates occurred at significantly larger values of the variable than did negative net growth rates (i.e., there is a positive correlation between the environmental variable and net growth). ''Grns'' = Greens (G1–G7); ''Dtms'' = Diatoms (D8–D24); BGs = Bluegreens (B28–B38); ''Flgs'' = Flagellates (M25, C26, C27, F39, F40); ''All'' = All taxa (1–41); ''BV'' = total biovolume. Frequencies are taken from the complete data set (Fig. 1).

| Variable | All | BV | Grns | Dtms | BGs | Flgs |
|---|---|---|---|---|---|---|
| P vars | 63 | 3 | 4 | 49 | 4 | 4 |
| SRSi | 10 | 1 | 0 | 9 | 0 | 1 |
| $NO_3$ | 12 | 1 | 1 | 10 | 0 | 1 |
| $\Sigma N$ | 7 | 0 | 2 | 1 | 4 | 0 |
| pH | 9 | 0 | 2 | 0 | 6 | 1 |
| ANC | 3 | 0 | 1 | 1 | 0 | 0 |
| $SD_{interp}$ | 12 | 1 | 1 | 9 | 1 | 1 |
| $Z_{mix}$ | 15 | 1 | 1 | 13 | 0 | 1 |
| Heat vars | 23 | 0 | 6 | 1 | 14 | 2 |
| Mean wind | 7 | 0 | 1 | 5 | 1 | 0 |
| $I_{mean}$ | 14 | 0 | 3 | 1 | 7 | 3 |
| *Diaptomus* | 21 | 0 | 6 | 5 | 8 | 1 |
| *Epischura* | 17 | 0 | 6 | 0 | 10 | 1 |
| Cyclopoids | 5 | 0 | 1 | 0 | 3 | 1 |
| *Diaphanosoma* | 2 | 0 | 0 | 0 | 2 | 0 |
| *Bosmina* | 3 | 0 | 0 | 0 | 3 | 0 |
| *Daphnia* | 14 | 0 | 3 | 0 | 11 | 0 |
| DgDt tot | 2 | 0 | 1 | 0 | 1 | 0 |
| *C. unicornis* | 5 | 0 | 2 | 0 | 2 | 1 |
| *C. hippocrepis* | 4 | 0 | 1 | 2 | 0 | 1 |
| Rotifers A | 16 | 0 | 1 | 2 | 13 | 0 |
| *Polyarthra* | 7 | 0 | 3 | 1 | 3 | 0 |
| *Ascomorpha* | 4 | 0 | 1 | 2 | 1 | 0 |
| Rotifers B | 16 | 0 | 3 | 2 | 9 | 2 |

Table 5. As Table 4, but listing the number of taxon-specific cases for each environmental variable when negative net growth rates occurred at significantly larger values of the variable than did positive net growth rates (i.e., there is a negative correlation between the environmental variable and net growth).

| Variable | All | BV | Grns | Dtms | BGs | Flgs |
|---|---|---|---|---|---|---|
| P vars | 17 | 0 | 4 | 0 | 11 | 2 |
| SRSi | 4 | 0 | 2 | 0 | 2 | 0 |
| $NO_3$ | 4 | 0 | 0 | 0 | 4 | 0 |
| $\Sigma N$ | 6 | 1 | 0 | 6 | 0 | 0 |
| pH | 11 | 1 | 0 | 11 | 0 | 0 |
| ANC | 3 | 0 | 1 | 0 | 1 | 1 |
| $SD_{interp}$ | 5 | 0 | 1 | 1 | 3 | 0 |
| $Z_{mix}$ | 10 | 0 | 3 | 1 | 6 | 0 |
| Heat vars | 29 | 1 | 1 | 25 | 1 | 2 |
| Mean wind | 5 | 0 | 0 | 0 | 3 | 2 |
| $I_{mean}$ | 8 | 0 | 0 | 8 | 0 | 0 |
| *Diaptomus* | 11 | 0 | 0 | 10 | 0 | 1 |
| *Epischura* | 19 | 2 | 0 | 19 | 0 | 0 |
| Cyclopoids | 8 | 1 | 0 | 7 | 0 | 1 |
| *Diaphanosoma* | 16 | 1 | 2 | 12 | 1 | 0 |
| *Bosmina* | 12 | 1 | 1 | 7 | 2 | 1 |
| *Daphnia* | 63 | 5 | 7 | 41 | 8 | 4 |
| DgDt tot | 13 | 1 | 3 | 8 | 2 | 0 |
| *C. unicornis* | 12 | 1 | 0 | 9 | 1 | 1 |
| *C. hippocrepis* | 2 | 0 | 1 | 0 | 1 | 0 |
| Rotifers A | 41 | 4 | 0 | 34 | 2 | 5 |
| *Polyarthra* | 13 | 1 | 1 | 10 | 0 | 2 |
| *Ascomorpha* | 1 | 0 | 0 | 1 | 0 | 0 |
| Rotifers B | 24 | 2 | 0 | 23 | 1 | 0 |

''*Daphnia*''; *Keratella, Kellicottia,* and *Notholca* were aggregated as ''Rotifers A''; and *Trichocerca, Ploesoma, Filinia,* and all *Synchaeta* were aggregated as ''Rotifers B.''

In every case among the aggregated variables there were no inconsistencies within the member categories in terms of statistically significant response patterns. Taxon-specific frequencies of positive or negative growth response to each environmental variable are listed in Tables 4 and 5. We used the full count of statistically significant responses identified in the complete data set (i.e., Fig. 1) but assigned the counts to aggregated variables subsequently identified. Summary taxon-specific fingerprints of the condensed environmental variable suite are illustrated in Fig. 2.

Frequency distributions reported in Tables 4 and 5 were tested for homogeneity across taxa by chi-squared analysis. Simultaneous analysis of four aggregated taxon categories (greens, diatoms, bluegreens, and flagellates) revealed striking inhomogeneities ($p = 6.1 \times 10^{-15}$ for positive growth rate correlations and $p = 1.1 \times 10^{-16}$ for negative growth rate correlations). Pairwise contrasts among the four taxon groups likewise revealed strong differences in response to environmental variables (Table 6). Extraordinarily strong statistical differences exist between diatoms and every other taxon as well as between bluegreens and flagellates during positive growth phases. These statistical differences refer to the patterns of effects by environmental variables. They carry an implicit assumption that it is valid to aggregate taxa by taxonomic division or functional group (e.g., flagellates).

Objective evidence for the claim that different environmental variables influence positive and negative growth phases is provided by chi-squared contrasts of the frequency data for positive and negative growth (Table 7). If environmental variables are aggregated into three categories (chemical variables, physical variables, and zooplankton variables; Table 8), it becomes clear that the striking differences between positive and negative net growth phases for the diatoms ($\chi^2 = 153$, df = 2, $p = 7.3 \times 10^{-34}$) result from predominating effects of positive correlations with chemical variables during positive growth and predominant effects of positive correlations with zooplankton variables during declines. Bluegreens ($p = 0.001$), on the other hand, demonstrate predominating significance by zooplankton during positive growth phases and elevated significance of chemical conditions during net negative growth. No statistically significant effects emerge for either greens or flagellates when the data are so aggregated.

*Modalities of algal response to environmental variables*—An illuminating alternative to aggregating algal taxa a priori by taxonomy is to group them by patterns of response to environmental variables. The patterns reported in Fig. 2 were coded numerically such that positive correlations (gray) were assigned the value ''1'' and negative correlations (black) were assigned ''−1.'' Nonsignificant relationships (white)

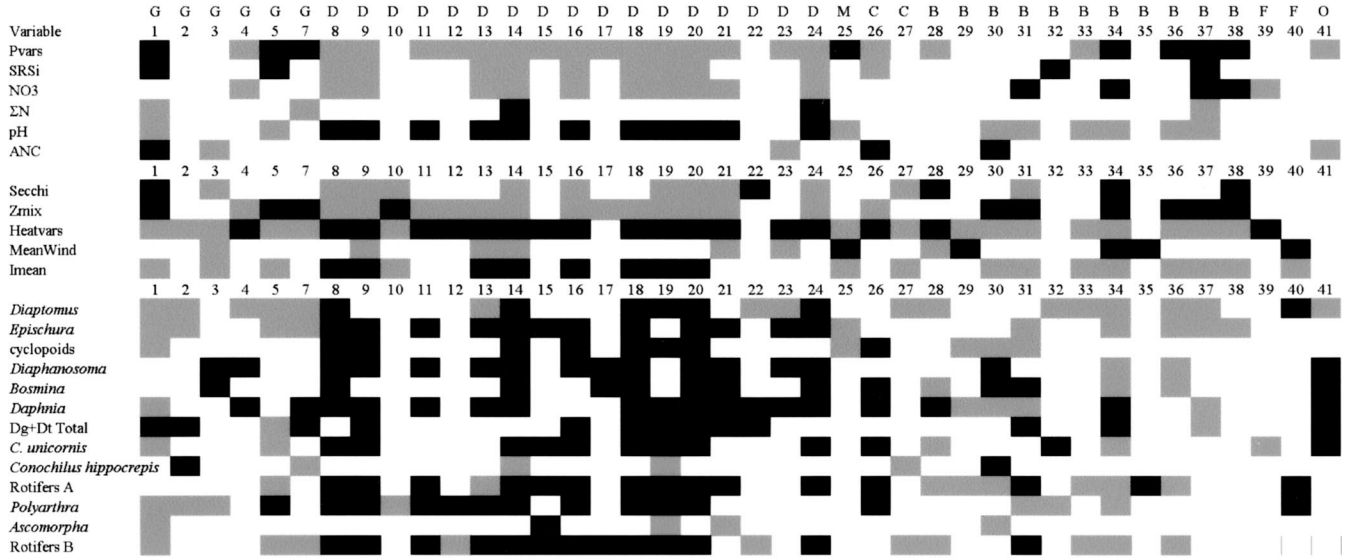


Fig. 2. As in Fig. 1, but environmental variable list has been condensed to conform more closely to the number of independent variables identified by principal components analysis.

were treated as missing values. Euclidean distances were calculated among all pairwise contrasts. Taxa were then sorted into clusters that exhibited minimal Euclidean distance differences among all members of the cluster. Finally, the clusters were inspected visually and were condensed to a set of six that displayed complete internal coherence with respect to both chemical and physical variables (Fig. 3).

Cluster A is dominated by four chlorophyte taxa and eight cyanophytes plus *Mallomonas* and *Synedra tenera.* Growth rates for these taxa are correlated positively (i.e., net growth is positive) with elevated lake heat, increased average light in the mixed layer, increased pH, increased concentrations of N species other than nitrate, and increasing abundances of all copepods. Growth rates correlate negatively (i.e., net growth is negative) with increasing phosphorus, silica, nitrate, water transparency, wind speeds, and mixed layer depth. This is equivalent to saying that positive net growth is associated with decreasing P, Si, $NO_3$, Secchi visibility, wind, and mixed layer thickness. The details of differences among the algal taxa trace entirely to idiosyncrasy of response to different Cladocera and rotifer taxa, with both positive and negative responses common on a species-specific basis.

Cluster B (B31, D10, C27) is otherwise similar to cluster A except that the three taxa have growth rates that correlate positively with water transparency. Cluster C (G3, B33, O41) differs further yet in that growth rates correlate positively with phosphorus, ANC, and wind speed, as well as with water transparency.

Cluster D is dominated by 13 diatom taxa plus *Chroomonas minuta.* These taxa are allied in exhibiting positive growth rates in response to elevated phosphorus, silica, nitrate, water transparency, mixing depth, and wind speed. Their net growth rates are negatively affected by increasing epilimnion heat content, average light in the mixed layer, pH, and N species other than nitrate. Their net growth rates are negatively associated, moreover, with elevated concentrations of all copepods and Cladocera as well as most rotifers. This assemblage exhibits highly monolithic response to chemical, physical, and biological variables.

Cluster E (gelatinous green algae, *Fragilaria, Synedra tenera*, *Anabaena*, and *Ceratium*) differs from cluster D mainly by exhibiting more positive responses to some zooplankton taxa, particularly *Diaptomus.* Some of the algal taxa in cluster E also exhibit negative growth responses with increased water transparency and concentrations of ammonia. Cluster F (dinoflagellates other than *Ceratium*) does not clearly conform to any of the other clusters, and so it sits alone.

The data do not permit resolution of statistically significant responses to all environmental variables for any of the algal taxa, and so the matrix of responses is underdetermined, causing some ambiguity of cluster assignments. *Synedra tenera,* for example, conforms with both cluster A and

Table 6. Chi-squared probabilities for tests of homogeneity between pairs of frequency distributions reported in Tables 4 and 5. "n.s." = not statistically significant at $\alpha = 0.05$.

| | Diatoms | | Bluegreens | | Flagellates | |
|---|---|---|---|---|---|---|
| | Pos-r | Neg-r | Pos-r | Neg-r | Pos-r | Neg-r |
| Greens | $1.5\times10^{-9}$ | $3.2\times10^{-14}$ | n.s. | n.s | n.s. | n.s. |
| Diatoms | | | $4.8\times10^{-21}$ | $4.6\times10^{-23}$ | 0.0002 | $1.9\times10^{-6}$ |
| Bluegreens | | | | | 0.02 | n.s. |

Table 7. Chi-squared probabilities for tests of homogeneity between frequency distributions for positive net growth rates and negative net growth rates as reported in Tables 4 and 5.

| | Probability |
|---|---|
| All taxa | $1.9\times10^{-14}$ |
| Greens | 0.02 |
| Diatoms | $2.9\times10^{-47}$ |
| Bluegreens | $3.8\times10^{-8}$ |
| Flagellates | n.s. |

cluster E because the available data do not resolve its growth responses to chemical variables (i.e., the contrasts between mean values of chemical variables during positive and negative growth phases are statistically insignificant in all cases).

We assessed the degree to which clusters merely represented taxa that exhibited contemporaneous correlations among abundances in situ. A correlation matrix was constructed for all pairwise combinations of 40 algal taxa, using logarithm-transformed biovolumes. For each algal taxon, the correlation matrix was sorted to rank pairwise correlations in decreasing order. For taxa belonging to clusters of size $n$, the top $n - 1$ correlations were surveyed to determine how many other members of the same cluster numbered among the set of top-ranked correlations. This analysis was designed to test whether clusters represented species that tend to increase or decrease at the same time. The results were tested against expectations for hypergeometric distributions drawing on a population pool of 40 taxa and sampling the numbers that appear in the clusters (Fig. 3). Results of this analysis are reported in Table 9. Of the 11 cases where cluster allies appear to exhibit contemporaneous correlations in biovolume that are higher than by random assortment, 10 are diatoms and all are from cluster D.

*Response to physical variables*—Algal divisions segregate well by mixing depth during net positive growth (Fig. 4a) but not by water transparency per se ($p = 0.16$). Neither of the two physical variables in Fig. 4 segregate taxa at the division level when cells are in negative net growth phases (Fig. 4b). Both mixed layer temperature and mean irradiance in the mixed layer do, however, segregate the divisions well during both positive (Fig. 5a: $p = 2 \times 10^{-6}$ for $T_{mix}$; $p = 0.0004$ for $I_{mean}$) and negative (Fig. 5b: $p = 0.007$ for $T_{mix}$ and $p = 0.04$ for $I_{mean}$) net growth rates.

Some statistically significant differences emerge at the division level between the mean values of physical factors associated with positive and negative growth phases by two-tailed paired $t$-test. Secchi transparency depth is different and higher during positive growth for diatoms ($p = 0.02$) but lower during positive growth for bluegreens ($p = 0.04$). Mixing depth is also higher during positive growth for diatoms ($p = 0.004$) and lower during positive growth for bluegreens ($p = 0.006$). Mixed layer temperatures are much cooler ($p = 0.0002$) when diatoms are in positive growth phases than when in decline for every taxon except D10 (*Cyclotella bodanica* + *C. comta*), consistent with the diatom reputation for success at low light and low temperatures (Talling 1957; Willén 1991). Mean light in the mixed layer was slightly elevated overall during positive growth for diatoms ($p = 0.048$), somewhat surprising in light of the admonition of Reynolds (1989) that the group is susceptible to photoinhibition. Among the bluegreens, mixed layer light intensities were generally lower during positive growth phases than negative ones ($p = 0.004$) for all taxa except *Aphanizomenon* and *Lyngbya.*

## Discussion

The community structure of phytoplankton in Lake Washington appears to sort out remarkably well with environmental variables. There are two major modes of growth rate variation in response to environmental conditions, with perhaps four additional variations on the major ones.

The most uniform growth response is one shared by most of the diatom species (cluster D). These allied species rise and fall in unison. They prosper when nutrients are elevated, mixing is deep, and the water is both cold and transparent. They are impeded by thermal stratification and by increasing abundances of virtually any zooplankton species. There is little qualitative in chemical, physical, or biological response that discriminates most of these species. The differences among taxa instead lie in the quantitative details of species-specific responses to resources, temperature, and light. *Synedra tenera* is a notable exception to this pattern. The species enters the plankton as an epiphyte, and it seems to have broken away from the typical diatom adaptive strategy.

A second major mode of growth response (cluster A) is exhibited by taxa endowed with motility or buoyancy. These species exploit nutrient-depleted and thermal stratified surface layers probably in part because as Reynolds (1983, 1984*a*,*b*, 1989, 1994) has theorized insightfully, they are loss minimizers. These species have common responses to chemical and physical variables, but they differ in response to zooplankton. They generally benefit from increasing numbers of copepods, but they exhibit species-specific responses to Cladocera and rotifers. These taxa do not bloom or suc-

Table 8. Frequencies at which environmental variables aggregated by category are statistically significant during either positive or negative growth phases by various taxon groupings.

| | Greens | | Diatoms | | Bluegreens | | Flagellates | |
|---|---|---|---|---|---|---|---|---|
| | Pos-r | Neg-r | Pos-r | Neg-r | Pos-r | Neg-r | Pos-r | Neg-r |
| Chem vars | 10 | 7 | 70 | 17 | 14 | 18 | 7 | 3 |
| Phys vars | 12 | 5 | 29 | 35 | 23 | 13 | 7 | 4 |
| Zoop vars | 28 | 15 | 14 | 181 | 66 | 18 | 7 | 15 |

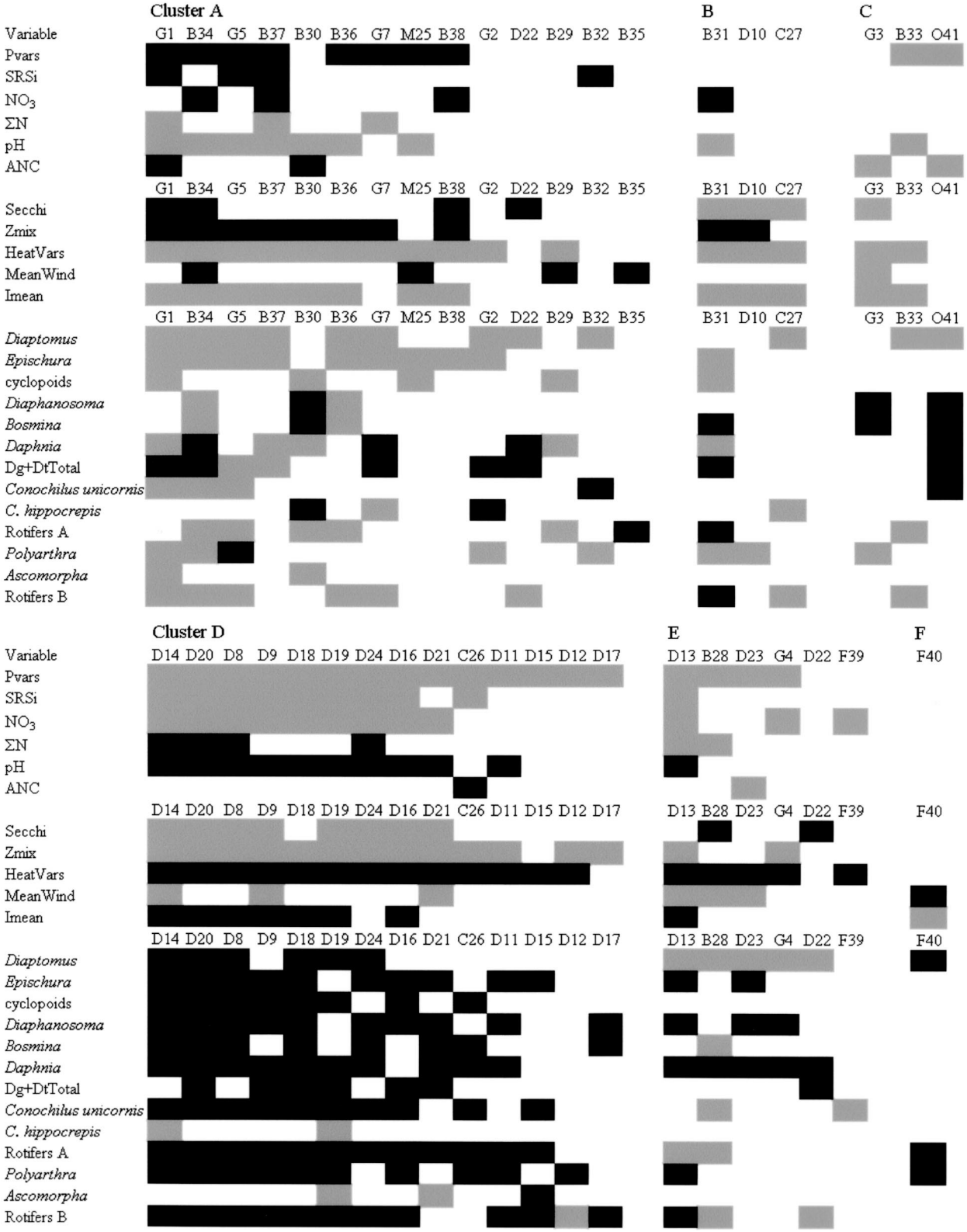


Fig. 3. As in Fig. 2, but taxa are assorted into six clusters segregated by coherence of response to chemical and physical environmental variables.

Table 9. Deviations of intertaxon biovolume correlations (ln transformation) from expected hypergeometric distributions with sample sizes set by the size of algal taxon clusters. ''Correlations'' = number of cluster allies that exhibit high contemporaneous correlation. ''n.s.'' = the number of allied taxa with high correlations does not exceed that expected by random sampling from the taxon pool.

| Taxon | Cluster | Correlations | *p* |
|---|---|---|---|
| G1 | A | 4 | n.s. |
| G2 | A | 3 | n.s. |
| G3 | C | 0 | n.s. |
| G4 | E | 3 | 0.010 |
| G5 | A | 5 | n.s. |
| G7 | A | 3 | n.s. |
| D8 | D | 8 | 0.010 |
| D9 | D | 8 | 0.010 |
| D10 | B | 0 | n.s. |
| D11 | D | 8 | 0.010 |
| D12 | D | 2 | n.s. |
| D13 | E | 1 | n.s. |
| D14 | D | 8 | 0.010 |
| D15 | D | 7 | 0.049 |
| D16 | D | 2 | n.s. |
| D17 | D | 3 | n.s. |
| D18 | D | 10 | $9.2\times10^{-5}$ |
| D19 | D | 8 | 0.010 |
| D20 | D | 7 | 0.049 |
| D21 | D | 5 | n.s. |
| D22 | A | 0 | n.s. |
| D22 | E | 2 | n.s. |
| D23 | E | 2 | n.s. |
| D24 | D | 8 | 0.010 |
| D25 | A | 1 | n.s. |
| C26 | D | 7 | 0.049 |
| C27 | B | 0 | n.s. |
| B28 | E | 1 | n.s. |
| B29 | A | 4 | n.s. |
| B30 | A | 1 | n.s. |
| B31 | B | 1 | n.s. |
| B32 | A | 1 | n.s. |
| B33 | C | 0 | n.s. |
| B34 | A | 3 | n.s. |
| B35 | A | 6 | n.s. |
| B36 | A | 4 | n.s. |
| B37 | A | 6 | n.s. |
| B38 | A | 3 | n.s. |
| F39 | E | 1 | n.s. |
| O41 | C | 1 | n.s. |

ceed contemporaneously, but rather may exhibit differential successes in different years.

For clusters A, B, and C physical and chemical conditions seem to set the stage for taxa that might succeed, but actual success is governed by the constellation of grazers, particularly cladoceran and rotifer grazers, that face the developing populations. There appears to be high specificity to the ways that individual grazers interact with individual algae in these clusters. Differential and complementary effects of crustacean grazers on phytoplankton have been reported (Burns and Schallenberg 2001; Sommer et al. 2001). There are in fact several cases within clusters A, B, and C where copepods exhibit positive correlations with growth rate while various cladocerans exhibit negative correlations. However, the differences do not break out cleanly as large versus small species as Sommer et al. report. Instead, the copepods are negatively associated with the cluster D species (almost all diatoms) and positively associated with most others. Detailed specificity of grazer interaction with net algal growth rates traces mainly to the cladocerans and rotifers. Those grazers thus represent a biological gamut that selects a contemporary species assemblage from a large pool of contenders.

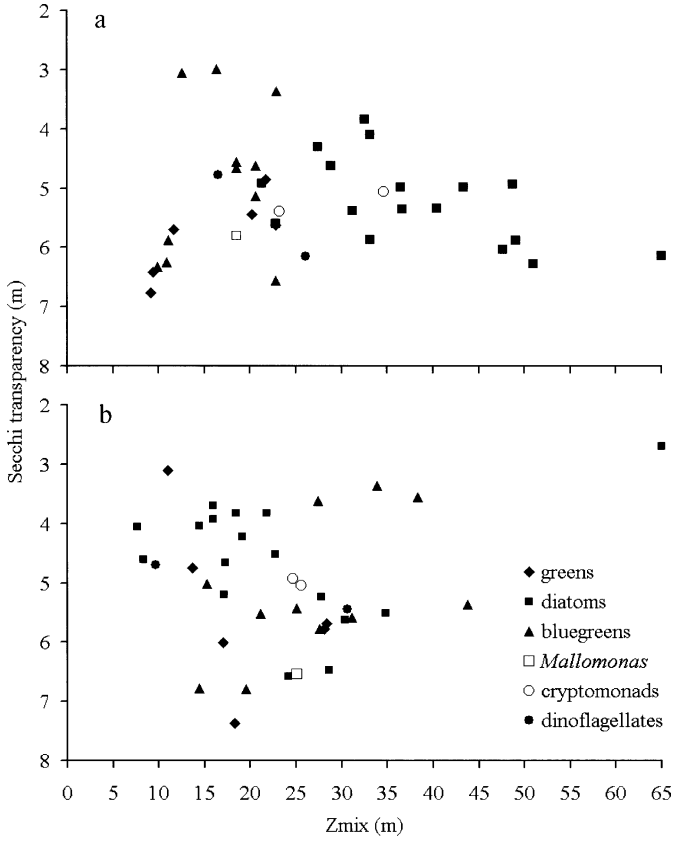


Fig. 4. Mean values of mixed layer depth and Secchi transparency depth during (a) positive or (b) negative net growth phases for Lake Washington algal taxa.

It is noteworthy that a relatively few algal taxa exhibit no negative net growth rate correlations with abundance of any zooplankton taxon. These include *Mallomonas* (M25), *Aphanizomenon* (B29), *Anacystis* and its allies (B36), *Aphanocapsa* and its allies (B37), *Lyngbya* (B31), *Oscillatoria limnetica* (B38), *Ceratium* (F39), and, surprisingly, *Cyclotella bodanica* + *C. comta* (D10) and *Cryptomonas* spp. (C27). Statistical power to detect differences for the *Cyclotella* species is weak because only two periods of sustained decline were identified in the entire data series. However, for *Cryptomonas* the power is excellent, with over 200 dates each of sustained increase or decrease. It is an empirical fact in Lake Washington that the abundances of grazing zooplankton are no different on average between times of net increase and net decrease for this taxon. For example, for all cases of positive net growth by *Cryptomonas* spp. when detectable abundances of *Daphnia* spp. were present in the

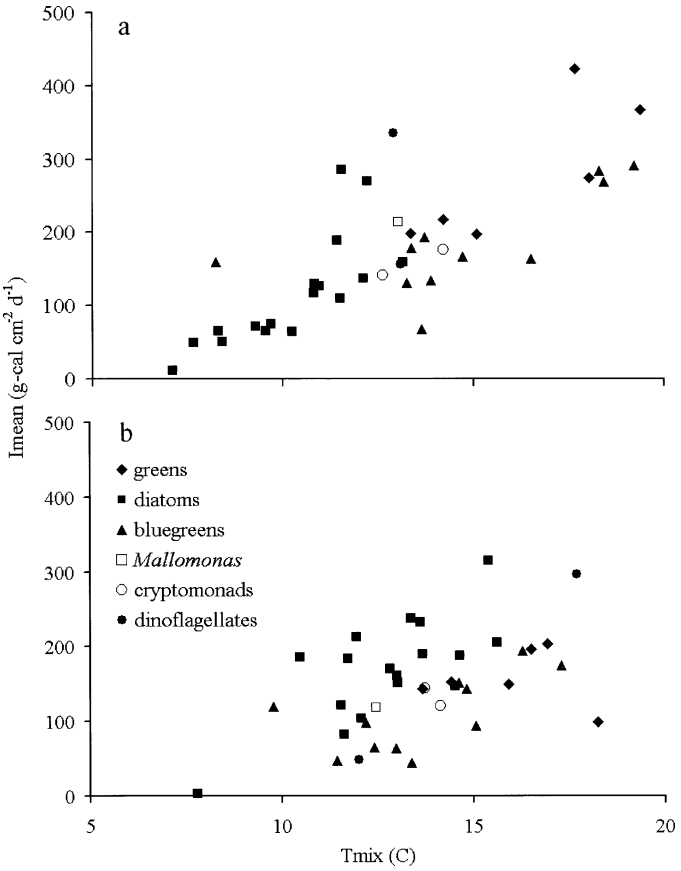


Fig. 5. Mean values of mixed layer temperature and index of mean irradiance in the mixed layer during (a) positive or (b) negative net growth phases for Lake Washington algal taxa.

lake, the mean ln abundance of *Daphnia* was 7.11 (SD = 2.37, $n = 128$); during net negative growth phases, ln *Daphnia* was 7.44 (SD = 2.16, $n = 85$).

The analysis documented in this report has a number of advantages for identifying environmental factors that are linked with population dynamics of algal taxa.

1. The selection of growth criteria is well defined, objective, and reproducible.

2. Environmental data that are extracted for analysis are confidently assigned to episodes of either positive or negative net growth.

3. Decisions about significance of effect are based on application of simple parametric statistics (e.g., *t*-test) to data that exhibit normal frequency distributions.

4. Inferences about the importance of different environmental factors during positive and negative growth phases are based on application of objective statistics to frequency data.

Part of the reason that environmental conditions differ between positive and negative growth phases for the various species is certainly that the algae transform the chemical and optical environment as they grow. They furthermore represent a food resource that permits herbivorous zooplankton to increase in abundance. The analysis presented here does not resolve the effects of the growing algae on environmental variables. It looks at the environmental conditions during growth and decline without attempting to explain how the different conditions evolved. By identifying the key factors associated with increases and declines of algal taxa, the analysis highlights variables that are most clearly related to growth rates as well as the modalities by which they interplay with the algae. This opens the way to subsequent analyses of the quantitative linkages among, for example, nutrient depletion or transparency declines and biomass accrual.

For example, the strongly negative associations between most diatoms and virtually all zooplankton species could be regarded as a consequence of the fact that zooplankton tend to increase in Lake Washington during late spring as the lake warms up and stratifies. This might threaten to be a case of correlation without causal connection. However, zooplankton need to exploit food resources as they grow, and diatoms are likely candidates for exploitation. It is a fair question for further study whether the grazing potential of the zooplankton at ambient abundances is consistent with the rates of decline of diatom biovolume at key times now identified.

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