

# Coexistence mechanisms and the paradox of the plankton: quantifying selection from noisy data

JEREMY W. FOX,<sup>1,3</sup> WILLIAM A. NELSON,<sup>2</sup> AND EDWARD MCCAULEY<sup>1,4</sup>

<sup>1</sup>*Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4 Canada*

<sup>2</sup>*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6 Canada*

**Abstract.** Many species of phytoplankton typically co-occur within a single lake, as do many zooplankton species (the “paradox of the plankton”). Long-term co-occurrence suggests stable coexistence. Coexistence requires that species be equally “fit” on average. Coexistence mechanisms can equalize species’ long-term average fitnesses by reducing fitness differences to low levels at all times, and by causing species’ relative fitness to fluctuate over time, thereby reducing differences in time-averaged fitness. We use recently developed time series analysis techniques drawn from population genetics to estimate the strength of net selection (time-averaged selection over a year) and fluctuating selection (an index of the variation in selection throughout the year) in natural plankton communities. Analysis of 99 annual time series of zooplankton species dynamics and 49 algal time series reveals that within-year net selection generally is statistically significant but ecologically weak. Rates of net selection are ~10 times faster in laboratory competition experiments than in nature, indicating that natural coexistence mechanisms are strong. Most species experience significant fluctuating selection, indicating that fluctuation-dependent mechanisms may contribute to coexistence. Within-year net selection increases with enrichment, implying that among-year coexistence mechanisms such as trade-offs between competitive ability and resting egg production are especially important at high enrichment. Fluctuating selection also increases with enrichment but is independent of the temporal variance of key abiotic factors, suggesting that fluctuating selection does not emerge solely from variation in abiotic conditions, as hypothesized by Hutchinson. Nor does fluctuating selection vary among lake-years because more variable abiotic conditions comprise stronger perturbations to which species exhibit frequency-dependent responses, since models of this mechanism fail to reproduce observed patterns of fluctuating selection. Instead, fluctuating selection may arise from internally generated fluctuations in relative fitness, as predicted by models of fluctuation-dependent coexistence mechanisms. Our results place novel constraints on hypotheses proposed to explain the paradox of the plankton.

**Key words:** *coexistence; competition; enrichment; paradox of the plankton; phytoplankton; selection; zooplankton.*

## INTRODUCTION

Many relatively isolated communities harbor multiple similar species, which co-occur over many generations. Hutchinson (1961) highlighted phytoplankton as a particularly striking example and coined the term “paradox of the plankton” to refer to the surprising co-occurrence of many phytoplankton within a single lake. Zooplankton comprise a second example, as many co-occurring zooplankton species compete strongly through a shared and limited prey community, and shared predators (reviewed in DeMott 1989, Grover 1997; see Plate 1). Nor is paradoxically high diversity

restricted to the species level. Many predominantly asexual planktonic species comprise multiple genotypes that exhibit substantial fitness differences in the lab (e.g., Loaring and Hebert 1981), but yet co-occur in the field (the “second paradox of the plankton”; Hebert and Crease 1983).

Long-term co-occurrence suggests stable coexistence. Stable coexistence requires that every species can increase when rare (Chesson 2000). As a result, coexisting species must all have long-term average per capita growth rates (fitnesses) of zero, since otherwise species would exhibit long-term trends in relative abundance that would eventually lead to exclusion (Levins 1979, Heino et al. 1998, Chesson 2000). Do plankton species actually satisfy this criterion on ecologically relevant timescales? Ecologists currently lack a quantitative answer to this basic descriptive question. This is an important gap in our understanding of community dynamics. For instance, explanations of

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<sup>3</sup> E-mail: jefox@ucalgary.ca

<sup>4</sup> Present address: Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA.

plankton coexistence that appeal only to mechanisms operating on within-year timescales, such as resource partitioning and trade-offs between competitive ability and predation resistance, are at least incomplete if plankton do not actually exhibit equal average fitness on these timescales (e.g., Tilman 1982, Leibold 1996, Grover 1997).

Many proposed solutions to the paradox of the plankton, including Hutchinson's (1961) own solution, appeal to fluctuations in relative fitness over time. For instance, if species' relative fitnesses depend on environmental conditions and the environment varies over time in an appropriate way, species' time-averaged fitnesses will be more similar than they would be if the environment remained in any one state (Hutchinson 1961, Lynch 1987). Species' relative fitnesses also will vary over time if fitnesses are frequency dependent and some intrinsic or extrinsic mechanism generates fluctuations in species' relative abundances (e.g., Hughes and Roughgarden 2000, Lehman and Tilman 2000). A large body of ecological theory addresses the conditions under which coexistence depends on temporal fluctuations in relative fitness (reviewed in Chesson 2000). However, in many communities, it is unknown whether species exhibit biologically significant fluctuations in relative fitness over time (but see Cáceres 1997, Adler et al. 2006). In many communities fluctuations in absolute abundance are positively correlated across species (Houlahan et al. 2007, Vasseur and Gaedke 2007), possibly indicating little temporal variation in relative abundance, and therefore in relative fitness.

Here we suggest a new approach for gaining quantitative insight into how species coexist, which draws on concepts and statistical tools from population genetics. From a theoretical perspective, coexisting species are analogous to coexisting genotypes of an asexual species. For clarity, and to emphasize the mathematical equivalence, we refer to the difference in fitness among both asexual genotypes and species as selection. Like community ecology, population genetics emphasizes that coexisting genotypes will display equal long-term average fitnesses (Heino et al. 1998). Population genetics also emphasizes the importance of quantifying variation in fitness among genotypes and over time as a necessary first step to identifying the underlying mechanisms generating this variation (Wright 1948, Heino et al. 1998). Our work is part of a broader recognition that community ecology and population genetics are closely analogous fields (Amarasekare 2000, Hubbell 2001, McPeck and Gomulkiwicz 2005).

We use statistical tools recently developed in population genetics to analyze time series of species abundances from natural algal and zooplankton communities in ponds and lakes. From these time series we estimate two quantities for each species: a net selection coefficient and a fluctuating selection coefficient. Selection for a given species is the difference between its per capita growth

and the per capita growth of all other species. Net selection is the time-average of selection experienced by a species. If all species are equally fit, on average, then we expect to observe no directional change in species' frequencies, and net selection will be zero for all species (note that neutral drift and migration should be negligible because plankton population sizes are very large and dispersal rates among lakes are low; Lynch 1987). Nonzero net selection implies either that some species are going extinct, or that longer term shifts in the direction of selection (on a timescale longer than that covered by the data) are crucial for coexistence. Fluctuating selection quantifies the amount of variation in selection over time that does not contribute to net selection. Fluctuating selection is large when a species sometimes experiences strongly positive selection, and sometimes experiences strongly negative selection. Previous studies use these and related statistical tools to quantify selection in time series of allele (Lynch 1987) and genotype (Nelson 2004) frequencies in *Daphnia* spp. To our knowledge, we are the first to apply these tools to time series of species frequencies.

Quantification of net and fluctuating selection allows novel comparative analyses of patterns in plankton dynamics. Plankton species richness and composition vary in predictable ways along gradients of key environmental variables such as enrichment (Watson et al. 1997, Dodson et al. 2000). However, patterns of variation in plankton dynamics are less well-known, particularly at the level of individual species as opposed to highly aggregated taxonomic groups. Selection dynamics may vary along environmental gradients because different species compositions coexist via different underlying mechanisms (e.g., fluctuation-dependent vs. fluctuation-independent mechanisms; Chesson 2000), and/or because environmental conditions directly affect selection dynamics, independent of species composition. Current hypotheses to explain patterns of variation in species composition and relative abundance along environmental gradients are largely silent on associated patterns of variation in dynamics (Tilman 1982, Leibold 1996, Grover 1997). By comparing patterns of net and fluctuating selection along environmental gradients to predictions of theoretical models, we test whether these models provide viable candidate solutions to the paradox of the plankton. To gain additional comparative insight, we also estimated selection in microcosm and mesocosm experiments designed to eliminate or control for key drivers of net and fluctuating selection in nature.

Our study complements much previous empirical work on plankton dynamics. Many studies of species interactions and temporal dynamics in lake plankton focus on the ecological mechanisms that might drive fluctuations in species abundances, and on seasonal variation in the strengths of these mechanisms (e.g., Sommer et al. 1986, Grover 1988, Gliwicz and Pijanowska 1989, Sommer 1989, 1990, Lampert and

Rothaupt 1991, MacIsaac and Gilbert 1991, Ives et al. 1999, Norberg 2000, Beisner 2001, Steiner 2003, Vasseur et al. 2005). Detailed studies of particular ecological mechanisms are essential for understanding plankton dynamics. Our focus is complementary: we examine the overall dynamical result of all the underlying ecological mechanisms operating on the timescales covered by our data in order to make cross-system comparisons. Analogously, in evolutionary biology, selection coefficients allow quantitative comparisons of evolutionary dynamics across species and traits, even though the underlying mechanisms generating selection are species and trait specific (Kingsolver et al. 2001). Previous quantitative studies of species-level plankton dynamics focus on describing patterns of covariation (synchrony and compensation) in absolute abundances (Vasseur et al. 2005, Keitt and Fischer 2006, Vasseur and Gaedke 2007). Our study differs in that we focus on the dynamics of relative rather than absolute abundance, which provides a direct measure of selection patterns.

We estimated net and fluctuating selection for a large number of highly resolved annual time series of phytoplankton and zooplankton dynamics from lakes spanning a wide range of sizes and environmental conditions. We focused on within-year dynamics, both because we lacked numerous lengthy multi-annual time series, and because co-occurrence of many plankton species over a single year is a sufficiently long period of apparent coexistence (often >50 generations) to require an explanation. Our results implicitly address the importance of coexistence mechanisms operating on longer timescales: nonzero net selection within a year implies that selection must fluctuate on multi-annual timescales in order for long-term coexistence to be maintained. We use our estimates of net and fluctuating selection coefficients to address the following questions. (1) How strong are net and fluctuating selection? That is, how close are species to equal average fitness on an annual timescale, and how much do relative fitnesses fluctuate within a year? (2) What underlying mechanisms govern the strength of net and fluctuating selection?

## METHODS

### *Estimating selection*

We estimate selection among species using methods developed by Nelson (2004) and Nelson et al. (2005), which we summarize here (see Appendix A for full details). The strength of natural selection can be estimated from the change in genotype or species relative abundance (frequency) through time (Lynch 1987). This is summarized by the coefficient of selection  $s_i(t)$ , which represents the difference between the per capita growth rate of species  $i$  at time  $t$ ,  $r_i(t)$ , and the per capita growth rate of the rest of the population,  $\bar{r}(t)$  (i.e.,  $s_i(t) = r_i(t) - \bar{r}(t)$ ). Selection at time  $t$  is calculated as

$$s_i(t) = \frac{dp_i(t)}{dt} \left\{ \frac{1}{p_i(t)[1 - p_i(t)]} \right\} \quad (1)$$

where  $p_i(t)$  is the relative abundance of species  $i$  at time  $t$ . Essentially, selection reflects how quickly frequencies are changing, modified by how close species are to loss or fixation.

The standard approach to estimating selection from time-series data is to calculate selection during a time step directly from observed changes in relative abundance from one time step to the next (Lynch 1987). However, this approach produces biased estimates of fluctuating selection when sampling error is overdispersed and selection coefficients are autocorrelated, as in plankton time-series data (see Appendix A for discussion). To obtain unbiased estimates of selection, we fit a statistical model to the observed time series of species counts, and then used Eq. 1 to calculate the selection coefficients from the fitted model. Since we have no a priori knowledge of how species' proportions should change over time, we chose a nonparametric regression model that makes no assumptions about the dynamics of species' proportions. The statistical model is

$$\frac{n_i(t)}{N(t)} = p_i(t) = f_i(t) \quad (2)$$

where  $n_i(t)$  is the observed count of species  $i$  at time  $t$  in a sample of size  $N(t)$ , and  $f_i(t)$  is a cubic spline representing the temporal dynamics of relative abundance. We used a Dirichlet-multinomial error distribution to allow for over dispersion, and calculated confidence intervals for the estimated selection coefficients for each species using parametric bootstrapping (see Appendix A for full details). This procedure correctly describes sampling error in the estimated selection coefficients (Eq. 1) as arising from (overdispersed) sampling error in the raw counts (i.e.,  $n_i(t)$  values).

Our fitting procedure simply describes the temporal dynamics of species' relative abundances, rather than attributing the dynamics to particular causes (e.g., Ives et al. 1999). In order to accurately describe temporal dynamics, we need to avoid possibly incorrect assumptions about the detailed ecological mechanisms producing those dynamics. We calculated selection dynamics,  $s_i(t)$ , from the estimated frequencies ( $p_i(t)$ ; Eq. 2) using Eq. 1. The estimated selection coefficients are per unit time ( $d^{-1}$ ). We did not attempt to estimate selection per generation because generation times vary among species, depend on temperature and other factors, and generally are unknown. The questions asked can be addressed equally well with per unit time coefficients.

The quantities of interest, net selection and fluctuating selection, are calculated by decomposing the fitted selection patterns,  $s_i(t)$ , for each lake-year (Nelson 2004, Nelson et al. 2005). Net selection on species  $i$  ( $S_{n_i}$ ) is the average selection acting on species  $i$  over the time period covered by the data:

$$S_{n_i} = \frac{\int_{t_1}^{t_2} s_i(t) dt}{t_2 - t_1} \quad (3)$$

where  $t_1$  and  $t_2$  are the first and last sampling days for a given lake in a given year. Fluctuating selection on species  $i$  ( $S_{fi}$ ) is the amount of selection on species  $i$  that does not contribute to net selection over the time period covered by the data, and is calculated as

$$S_{fi} = S_{pi} - |S_{ni}| \quad (4)$$

where

$$S_{pi} = \frac{\int_{t_1}^{t_2} |s_i(t)| dt}{t_2 - t_1} \quad (5)$$

is potential selection, the cumulative amount of selection (positive and negative) experienced by species  $i$  between times  $t_1$  and  $t_2$ . This definition of fluctuating selection quantifies the variation in the temporal selection pattern, and is analogous to estimating fluctuating selection from the variance of a distribution of selection coefficients (Lynch 1987).

Net selection and fluctuating selection are summarized for each lake-year as weighted means across species (Spitze 1991):

$$S_n = \sum_i |S_{ni}| \bar{p}_i \quad (6a)$$

$$S_f = \sum_i S_{fi} \bar{p}_i \quad (6b)$$

where the weight  $\bar{p}_i$  is the mean proportion of species  $i$  over the time series. Taking weighted means across species rather than unweighted means is necessary because fitness and selection are defined on a per capita basis, not a per species basis (Eq. 1). Mean net selection (Eq. 6a) is expressed as the weighted mean of the absolute values of the net selection coefficients because the net selection coefficients can be positive or negative. In Eq. 6b, taking absolute values is unnecessary because fluctuating selection coefficients are nonnegative by definition. The standard errors of these weighted means are calculated according to Sokal and Rohlf (1994:133).

Statistical significance of the estimated selection coefficients is not the same as ecological significance. Observed selection coefficients might be statistically significant but ecologically small. A sense of the ecological significance of selection can be gained by considering the time to competitive exclusion under a given rate of net selection. Since selection is modeled as a continuous process, time to complete exclusion is infinite. It is common practice to instead consider the time to quasi-loss, which is when a competitor has been reduced to a frequency of 0.01 (Lynch 1987). Time to quasi-loss ( $\tau_q$ ) is defined as the time it would take a competitor to go from an initial frequency  $\bar{p}(0)$  to a frequency of 0.01 under a constant selection rate of net selection  $S_n$ , and is given by the following relationship (Lynch 1987):

$$\tau_q = \frac{\ln \left[ \frac{1 - \bar{p}(0)}{\bar{p}(0)} \right] - \ln \left( \frac{1 - 0.01}{0.01} \right)}{S_n} \quad (7)$$

Our approach has sufficient statistical power to detect typical strengths of selection (Kingsolver et al. 2001; and see *Results*).

### Data

We analyzed 99 zooplankton lake-years, and 49 algal (phytoplankton) lake-years of data. Data came from three sources: the North Temperate Lakes Long-Term Ecological Research program in Wisconsin, USA ("LTER" data), the Experimental Lakes Area in northwestern Ontario, Canada ("ELA" data), and Lake Constance in central Europe, between Germany, Austria, and Switzerland ("LC" data). These data comprise some of the highest quality, most temporally and taxonomically detailed plankton time series in the world. The lakes vary widely in enrichment, size, and other variables (Appendix B).

The raw data were time series of species' relative abundances and sampling effort. Sampling effort is the number of individuals counted,  $N(t)$  in Eq. 2, which determines how much variation in the data reflects sampling error. Data were collected according to consistent protocols (slightly different protocols for ELA, LTER, and LC data), minimizing biases that might arise from variation in sampling protocols and species identification procedures. Dodson et al. (2000) and Gaedke and Schweizer (1993) provide details of sampling protocols. Sampling effort ranged from 200 to 800 individuals/sample in the ELA and LTER data, and from 231 to 9720 individuals/sample (mean 1825) in the LC data. Individuals were identified to the lowest taxonomic level possible (typically species level). In a few cases, different morphotypes of the same species were tracked separately in the original data, but we treated these as a single species. For phytoplankton species that can exist as both multicellular colonies and as single cells (e.g., *Dinobryon sertularia*), we expressed abundance as total number of cells.

We analyzed time series of relative abundances, rather than relative biomasses, because it is individual organisms, not units of biomass, that reproduce and die and so are subject to selection. Further, sampling error attaches to counts of individuals rather than units of biomass, so properly accounting for sampling error requires conducting the analysis in terms of relative abundances. Converting abundances to biomasses is not required for our purposes. We treated each lake-year as a separate, independent data set to focus on within-year coexistence. We recognize that different years from the same lake may be nonindependent, but such nonindependence would not alter our main conclusions (see *Results*).

All ELA and LTER lake-years comprised 9–17 samples, with samples typically separated by 7–14 days

during the local growing season. Samples thus were separated by about one generation for many zooplankton species during the growing season, and somewhat greater than one generation for phytoplankton. Samples outside the growing season typically were separated by >28 days. Most LC lake-years comprised 37–43 samples, with samples separated by about seven days during the growing season and about 14 days during the winter. Inspection of the data indicated that temporal variation in relative abundances was concentrated during the growing season, and it is these changes that generate most of the selection in any lake-year. Restricting analysis to samples taken during the growing season did not qualitatively alter the results (not shown).

The numerical fitting procedure failed to converge when a lake-year included many rare species. This was more often the case for phytoplankton than for zooplankton due to the higher species richness of the phytoplankton. Further, sampling error dominated the observed dynamics of rare species, preventing precise and accurate estimation of selection coefficients for rare species. We therefore combined all species that never attained 10% relative abundance in any sample within a lake-year into a single “rare” species. The 10% “rarity” threshold was the lowest feasible; lower thresholds caused fitting failure for some lake-years. Reanalyzing a subset of the data using a 6% rarity threshold leads to lumping of fewer species, but did not qualitatively alter the results and produced only minor quantitative changes (not shown).

For some LC lake-years, bootstrapping frequently generated very low densities for some species, causing the fitting procedure to fail. We therefore added one to the estimated density of every species in every sample in the LC data, so that the minimum density a species could exhibit was one individual/sample rather than zero. For consistency, we also increased the sampling effort by an amount equal to the species richness of the lake-year. This procedure slightly biased the relative abundance of rare species upwards, but produced only very minor quantitative changes in the estimated selection coefficients.

To test the hypothesis that fluctuating abiotic conditions generate fluctuating selection (Hutchinson 1961), and to identify novel drivers of selection, we regressed mean absolute net selection and mean fluctuating selection on five environmental variables and one methodological variable. The environmental variables were temporal mean and variance of water temperature, temporal mean and variance of pH, and enrichment (temporal mean concentration of total phosphorus [TP] in surface water). Water temperature and pH on each sampling date were depth-averaged over the epilimnion. We chose these variables because of their strong effects on physiology, species richness, and composition (Watson et al. 1997, Dodson et al. 2000, Fischer et al. 2001), and included temporal variances to test the classic hypothesis that variability in abiotic

conditions produces fluctuating selection that interrupts competitive exclusion (Hutchinson 1961). The methodological variable was the length of the sampling period (days between initial and final sample of phytoplankton or zooplankton). We included this variable to control for the fact that sampling periods varied in length, with ELA sampling periods (length =  $162 \pm 17$  d [mean  $\pm$  SD]) being shorter than LTER ( $283 \pm 34$  d) and LC sampling periods ( $321 \pm 43$  d). Insofar as fluctuating selection arises from seasonal variation in relative fitness, shorter sampling periods may truncate some of this seasonal variation, leading to biased estimates of net and fluctuating selection for the entire lake-year.

Some lake-years could not be used in the multiple regressions because we lacked data on one or more environmental variables. Response variables were square-root transformed to improve normality and homoscedasticity. Inspection of residuals indicated conformity with statistical assumptions. Variance inflation factors were <10 (typically <5), indicating no substantial multicollinearity of predictor variables (Kutner et al. 2004).

## RESULTS

Fig. 1a shows an algal lake-year (ELA Lake 239 in 1998), along with illustrative model fits (Eq. 2) to several bootstrap replicates. Variation among the fits arises from variability among bootstrapped lake-years due to sampling error and other unidentified error sources (overdispersion). Fig. 1b shows the estimated net and fluctuating selection coefficients for each species, along with bootstrapped 95% confidence intervals. Three of eight species experience net selection significantly different from zero at the  $\alpha = 0.05$  level, and all eight experience significant fluctuating selection. Clearly, 11 significant selection coefficients out of a possible 16 is unlikely due to chance alone. These results are typical for both phytoplankton and zooplankton. On average, approximately half the species in a lake-year experience significant net selection, and over 90% experience significant fluctuating selection.

By calculating mean absolute net selection and mean fluctuating selection across all species in a lake-year (Eq. 6), we obtain overall measures of net and fluctuating selection, which can be compared across lake-years. Phytoplankton and zooplankton exhibit relatively weak net selection (Fig. 2). Mean absolute net selection coefficients range from 0.002 to 0.027 d<sup>-1</sup> for phytoplankton and 0.001 to 0.021 d<sup>-1</sup> for zooplankton (Fig. 2). To put these numbers in context, a net selection coefficient of -0.007 (a typical negative value for both phytoplankton and zooplankton) leads to quasi-loss in ~343 days, assuming an initial community of 10 species (see Eq. 7; an average lake-year comprises 10 species after lumping of rare species). This time period is approximately one year, and longer than a single growing season, indicating that within-year coexistence mechanisms are sufficiently strong to maintain plankton

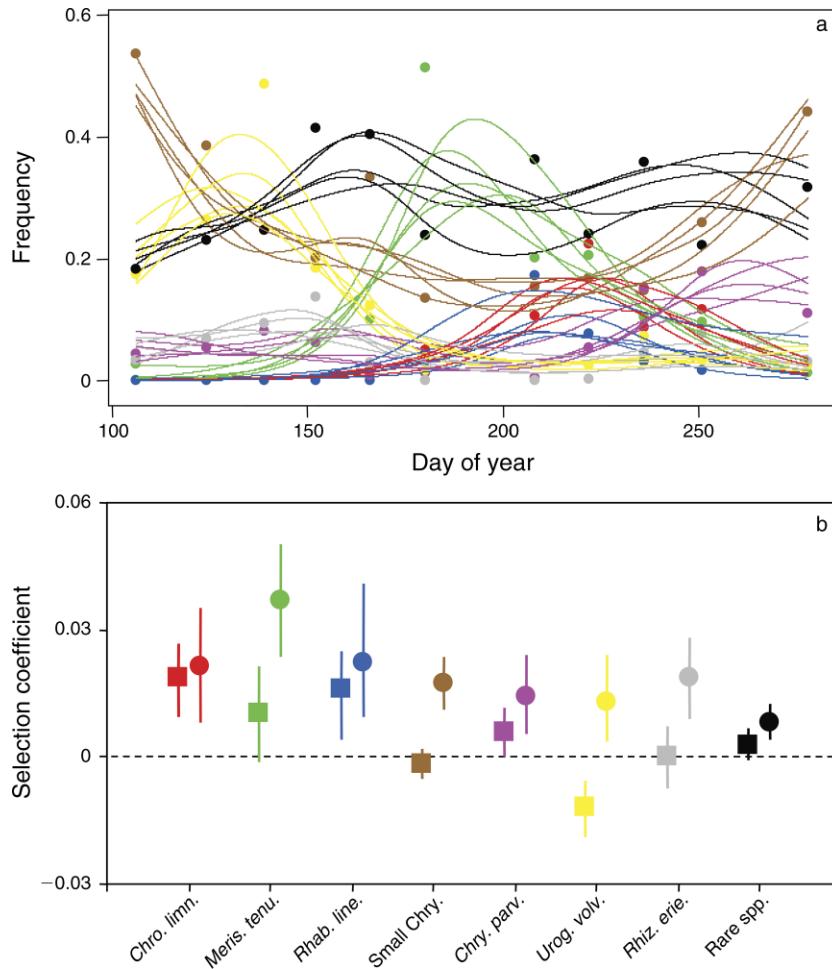


FIG. 1. (a) Observed algal species proportions (points) over time in ELA Lake 239 (Experimental Lakes Area, northwestern Ontario, Canada) in 1998, along with five illustrative bootstrap model fits (Eq. 2, lines). Sampling effort was 400 individuals/sample. Bootstrapped data points are omitted for clarity. Different colors indicate different species: red, *Chroococcus limneticus*; green, *Merismopedia tenuissima*; blue, *Rhabdogloea lineare*; brown, small Chrysophyceae; purple, *Chrysochromalina parva*; yellow, *Uroglena volvox*; gray, *Rhizosolenia eriensis*; black, rare spp. (b) Estimated net selection coefficients (squares) and fluctuating selection coefficients (circles) for each species, with 95% parametric bootstrap confidence intervals. Colors indicate different species, as in panel (a).

diversity for many generations, although not for arbitrarily long periods (since net selection often is significantly different from zero).

With one exception, mean absolute net selection is  $>0.015 \text{ d}^{-1}$  only in lake-years from ELA Lake 227 (Fig. 2). A net selection coefficient of  $-0.015 \text{ d}^{-1}$  implies quasi-loss in  $\sim 160$  days from an initial community of 10 species. Since 160 days is less than a single growing season, many species in ELA Lake 227 would be lost rapidly if the observed within-year net selection were not counterbalanced by longer term shifts in the direction of net selection.

Weak net selection does not necessarily imply strong coexistence mechanisms; species might simply be intrinsically similar. While we cannot directly estimate how strong net selection would be in the absence of any coexistence mechanisms, an indirect estimate is provided

by laboratory competition experiments (Tilman 1982, Grover 1997). Such experiments often are explicitly designed to minimize or eliminate all coexistence mechanisms. These experiments therefore provide a rough estimate of how strong net selection would be in nature in the absence of any coexistence mechanisms. In laboratory experiments in which phytoplankton or zooplankton are forced to compete for a single limiting resource in a well-mixed chemostat, the time to quasi-loss typically is  $\sim 10\text{--}50$  days (Tilman 1982, Gilbert 1985, MacIsaac and Gilbert 1989, 1991, Boraas et al. 1990, Grover 1997, Passarge et al. 2006). Assuming a mean initial frequency of 0.5 (i.e., a two-species experiment), quasi-loss in  $10\text{--}50$  days implies that the inferior competitor experiences a net selection coefficient between  $-0.4 \text{ d}^{-1}$  and  $-0.09 \text{ d}^{-1}$ ,  $>10$  times faster than observed in nature.

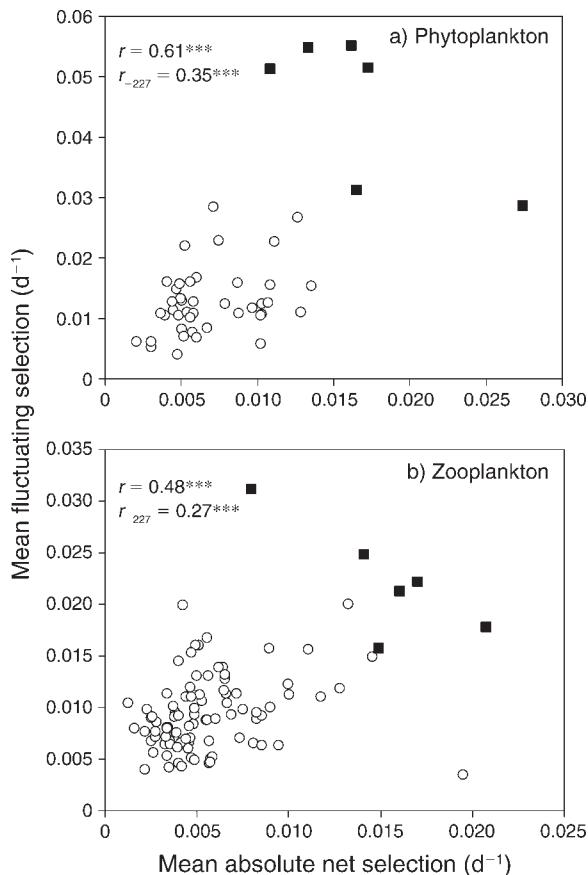


FIG. 2. Mean fluctuating selection ( $d^{-1}$ ) vs. mean absolute net selection ( $d^{-1}$ ) for (a) phytoplankton and (b) zooplankton (SE was calculated, but was so small that error bars are hidden by plot symbols). Solid squares indicate lake-years from experimentally enriched ELA Lake 227; open circles indicate lake-years from other lakes. The  $r$  values are correlation coefficients;  $r_{-227}$  values are correlation coefficients without ELA Lake 227 lake-years.

\*\*\*  $P < 0.001$ .

Mean fluctuating selection coefficients range from 0.004 to 0.055  $d^{-1}$  for phytoplankton and from 0.003 to 0.031  $d^{-1}$  for zooplankton (Fig. 2). Interestingly, mean absolute net selection and mean fluctuating selection are significantly positively correlated across lake-years in both phytoplankton and zooplankton (Fig. 2). This correlation is not an artifact of the fitting procedure, as it is simple to generate artificial data that exhibit no net selection and strong fluctuating selection, or vice versa (not shown). The positive correlations are driven in part by lake-years from ELA Lake 227, and become weaker (but remain significant) if these lake-years are dropped from the analysis (Fig. 2). The correlations in Fig. 2 remain significant if data from the same lake in different years are averaged and the analysis is conducted on the resulting lake means (not shown).

The correlations in Fig. 2 apparently reflect the fact that net and fluctuating selection respond similarly to

key environmental variables. For phytoplankton, multiple regressions on key environmental and methodological variables explain significant fractions of the variation in both mean absolute net selection and mean fluctuating selection (net selection:  $R^2 = 0.59$ ,  $F_{6,34} = 8.03$ ,  $P < 0.001$ ; fluctuating selection:  $R^2 = 0.76$ ,  $F_{6,34} = 17.63$ ,  $P < 0.001$ ). Net selection in phytoplankton increases significantly with mean temperature (Fig. 3a), while fluctuating selection increases significantly with mean temperature and enrichment (Fig. 3b, c).

For zooplankton, multiple regressions on key environmental and methodological variables explain significant fractions of the variation in both mean absolute net selection and mean fluctuating selection (net selection:  $R^2 = 0.73$ ,  $F_{6,65} = 25.79$ ,  $P < 0.001$ ; fluctuating selection:  $R^2 = 0.61$ ,  $F_{6,65} = 17.28$ ,  $P < 0.001$ ). Net selection in zooplankton increases significantly with enrichment, and decreases significantly with mean temperature, mean pH, and sampling period length (Fig. 4a–d). Fluctuating selection in zooplankton increases significantly with enrichment and mean temperature, and decreases significantly with sampling period length (Fig. 4e–g).

## DISCUSSION

### *How strong are net and fluctuating selection?*

Much previous work on the paradox of the plankton takes for granted the paradox itself: many species of plankton do indeed coexist indefinitely and therefore exhibit equal fitness on average. Further, many proposed resolutions of the paradox of the plankton appeal to coexistence mechanisms operating on within-year timescales, which would be expected to make species equally fit on those timescales (Hutchinson 1961, Tilman 1982, Leibold 1996, Grover 1997). Our results show that plankton species are not equally fit on within-year timescales, although they are close: the estimated mean time to quasi-loss in a typical lake is about one year, broadly consistent with the assumption that plankton coexist on within-year timescales. Note however that even the weak net selection observed in most lakes is too strong to be considered “near neutral” (see below in this subsection).

Evidence from lab experiments suggests that net selection is weak because within-year coexistence mechanisms are strong, not because plankton species are intrinsically similar. Laboratory competition experiments, which often use species known to coexist in nature, reveal rates of net selection  $>10$  times faster than observed in nature. Laboratory experiments eliminate extrinsic abiotic variation and many sources of intrinsic temporal variation, modify average environmental conditions, remove the background community, and simplify the resource base. All of these modifications might increase rates of net selection above those observed in nature.

It is easy to imagine that the weak within-year net selection observed in nature could be counterbalanced in

the long run by year-to-year changes in the direction of net selection or trade-offs between competitive ability and resting egg production (Nelson 2004). Evolutionary studies frequently find long-term shifts in the direction of selection (Hoekstra et al. 2001), and such shifts may be common in ecology as well. Longer term processes must be crucial to the long-term maintenance of diversity in those rare lakes in which within-year net selection is strong.

Fluctuating selection is common: ~90% of the plankton species in a typical lake experience significant within-year fluctuating selection. Our estimates of within-year fluctuating selection represent a lower bound because we cannot detect fluctuating selection at timescales shorter than the sampling interval. In many lake-years, plankton were sampled at monthly or semimonthly intervals during the growing season. This sampling frequency might miss short-term fluctuations in selection arising from perturbations such as storms.

Continuing the theme of using tools from evolutionary dynamics to provide insight into ecological dynamics, our results show that plankton dynamics are not purely neutral. A rule of thumb in population genetics is that selection dominates neutral drift when  $s \gg 1/N_e$ , where  $s$  is the selection coefficient and  $N_e$  is the effective population size. The mean absolute net selection coefficients observed in natural plankton communities are sufficiently large to dominate drift when  $N_e$  exceeds ~200–500 individuals. The total abundance of all phytoplankton, or all zooplankton, in a lake is always many orders of magnitude higher than this, and so selection dominates drift in all our lake-years. Our results contrast with the finding that some plankton species abundance distributions are consistent with neutral models (Walker and Cyr 2007), presumably because species abundance distributions provide only an information-poor snapshot of community structure equally consistent with neutral and nonneutral models. Much recent work in ecology attempts to reject the “null hypothesis” of neutrality using indirect methods such as fitting alternative models to the species abundance distribution (McGill et al. 2006). We believe our approach is more informative, in that it directly estimates how close species are to equal average fitness, and how much relative fitnesses fluctuate over time, rather than simply attempting to reject the null hypothesis of neutrality via indirect means.

*What underlying mechanisms govern the strength of net and fluctuating selection?*

Our approach classifies coexistence mechanisms by their effects on species' fitness, rather than by the conditions required for their operation. In particular, fluctuating selection does not necessarily imply an important role for fluctuation-dependent coexistence mechanisms, sensu Chesson (2000). However, absence of fluctuating selection on the timescales considered here would imply the absence of such coexistence mecha-

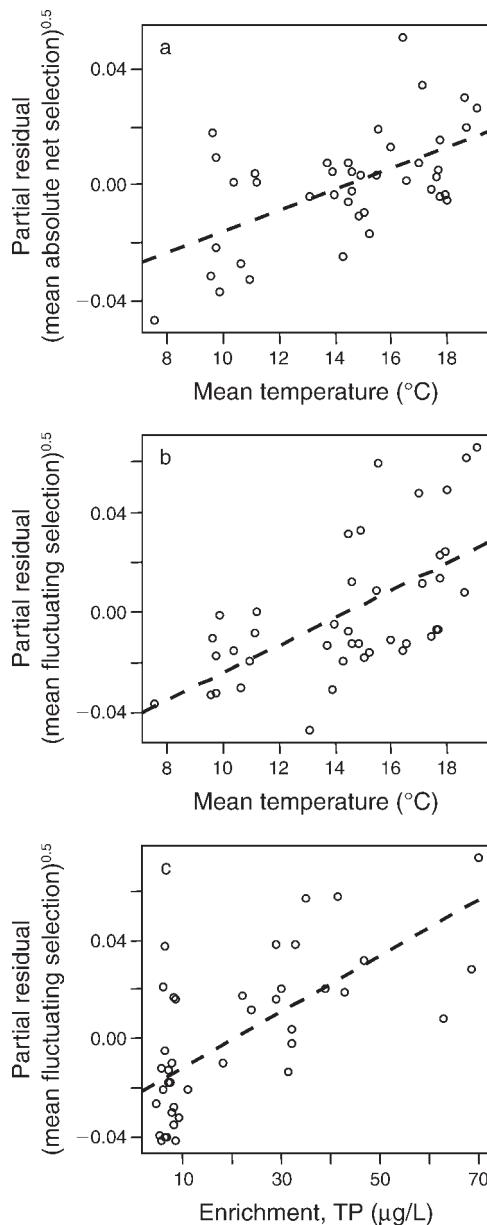


FIG. 3. Partial residual plots of (a) mean absolute net selection and (b–c) mean fluctuating selection vs. predictor variables. Enrichment indicates the temporal mean concentration of total phosphorus (TP) in surface water. Dependent variables were square-root transformed (i.e., by raising that quantity to the 0.5 power). Each point gives the value of  $\beta_i x_i + e$  as a function of  $x_i$ , where  $x_i$  is the  $i$ th predictor variable from a multiple regression,  $\beta_i$  is the estimated partial regression coefficient of the dependent variable on the  $i$ th predictor variable, and  $e$  is the residual from the multiple regression. The dashed line shows the partial regression relationship,  $\beta_i x_i$ .

nisms on those timescales. Cáceres (1997) demonstrated that the storage effect promotes the persistence of a single *Daphnia* species in a single lake. Our work provides the first rigorous demonstration that fluctuation-dependent coexistence mechanisms such as relative

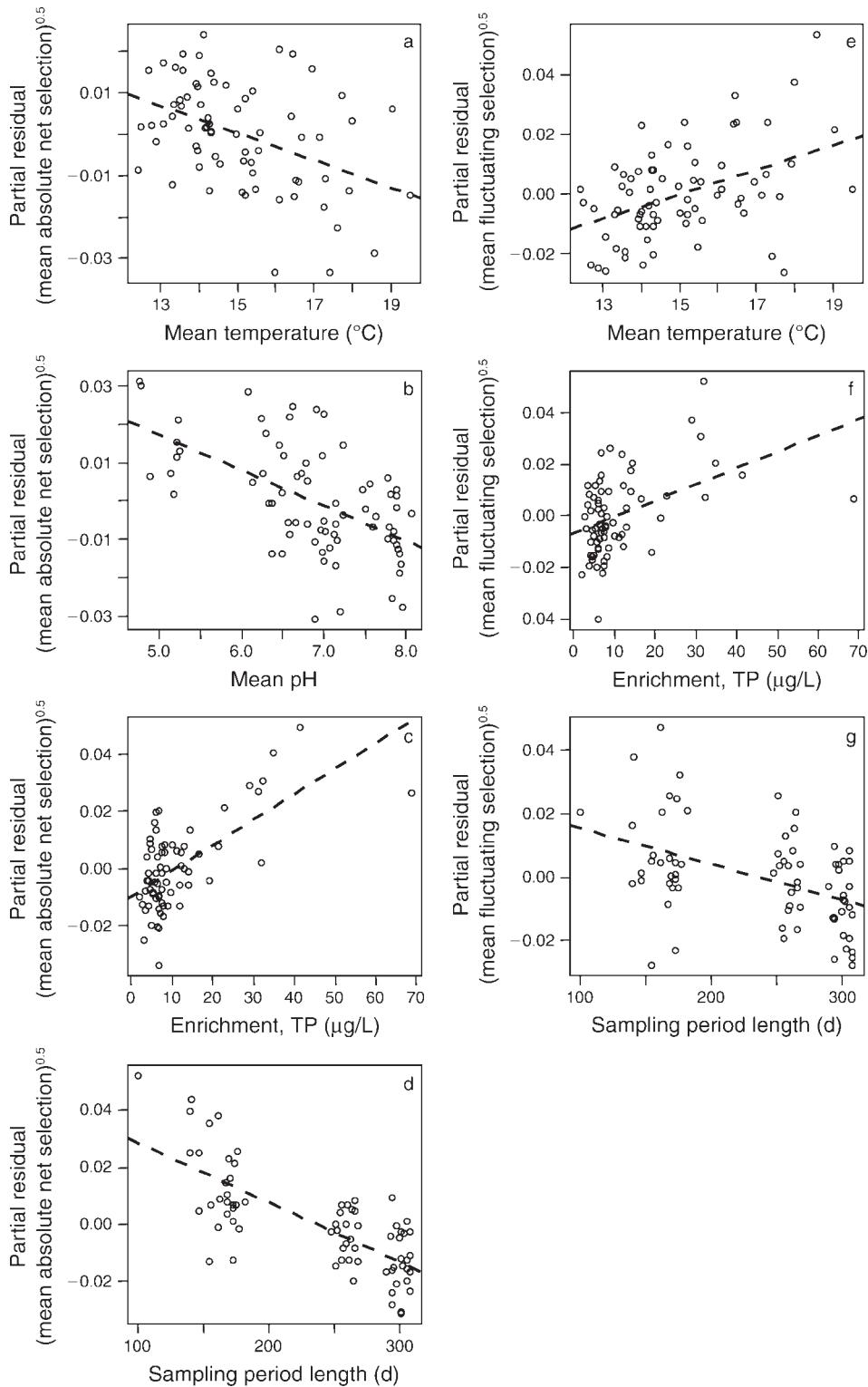


FIG. 4. Partial residual plots of mean absolute net selection (a–d) and mean fluctuating selection (e–g) vs. predictor variables. Dependent variables were square-root transformed. Points and lines are as in Fig. 3.



PLATE 1. *Daphnia pulicaria*, a common zooplankton species in several of the data sets analyzed here. Photo credit: Shirley French and Almira Siew.

nonlinearity and the storage effect are viable candidate mechanisms to explain the coexistence of many species across a wide range of lakes (Armstrong and McGehee 1980, Huisman and Weissing 1999, Anderies and Beisner 2000, Chesson 2000). Next we draw on several lines of evidence to evaluate in more detail the candidate mechanisms governing the strength of net and fluctuating selection.

Net and fluctuating selection for both phytoplankton and zooplankton increase with enrichment, while mean temperature has significant but inconsistent effects. Increasing rates of selection with increasing mean temperature are expected given that biological rates increase with temperature. Lower mean temperatures should act as an equalizing coexistence mechanism by slowing population growth rates, thereby reducing absolute rates of net selection and prolonging the absolute time to competitive exclusion (Chesson 2000). Rates of net and fluctuating selection in phytoplankton, and fluctuating selection in zooplankton, increase with increasing mean temperature as expected. However, rates of net selection in zooplankton actually decline with increasing mean temperature, indicating that the effects of temperature are not as simple as hypothesized.

Increasing net selection with increasing enrichment indicates that enrichment directly or indirectly weakens the collective strength of all coexistence mechanisms operating on within-year timescales. This is a novel result. Previous work suggests that the relative importance of different within-year coexistence mechanisms may vary with enrichment (e.g., Tilman 1982, Leibold 1996, Grover 1997). However, to our knowledge, no previous study suggests that the collective strength of all

within-year coexistence mechanisms might vary with enrichment.

The effects of enrichment identified by the multiple regressions are somewhat challenging to interpret because enrichment covaries with many other factors in nature, including species composition. Even in experimentally enriched ELA Lake 227, it is unclear if strong fluctuating selection represents a direct effect of enrichment on species' dynamics, an indirect effect mediated by changes in species composition, or both. Many mesocosm experiments manipulate enrichment while holding species composition constant, but few such experiments sample population dynamics with sufficiently fine temporal resolution to allow estimation of fluctuating selection. One such experiment is that of Mackey (1992). This experiment followed dynamics of rotifers and *Daphnia* in low- and high-enrichment mesocosms in a greenhouse (see Appendix C for details of experimental and analytical methods). Holding the initial species composition and other environmental

TABLE 1. Mean absolute net selection and mean fluctuating selection in the mesocosm experiment of Mackey (1992).

Enrichment	Replicate	Mean absolute net selection ( $d^{-1}$ )	Mean fluctuating selection ( $d^{-1}$ )
Low	1	0.0089	0.0397
	2	0.0096	0.0572
	3	0.0129	0.0301
High	1	0.0070	0.0601
	2	0.0056	0.0617
	3	0.0020	0.0693

Notes: There were three replicate mesocosms at each enrichment level. See Eq. 6 and its derivation for definitions of selection and explanation of units.

factors constant allowed the experiment to isolate the direct effect of enrichment on selection. Mean absolute net selection did not vary greatly with enrichment in this experiment, but mean fluctuating selection was  $\sim 50\%$  stronger at high enrichment (Table 1; Appendix C).

The results of Mackey (1992) suggest that increasing net selection with increasing enrichment is an indirect effect of enrichment mediated by shifts in species composition. Passarge et al. (2006) found that enrichment directly reduced net selection in algal communities maintained in chemostats, providing further support for the hypothesis that natural enrichment increases within-year net selection indirectly by shifting species composition. In contrast, the results of Mackey (1992) suggest that enrichment directly increases fluctuating selection. Testing the mechanisms by which enrichment affects fluctuating selection would be an interesting direction for future work. Enrichment might directly increase fluctuating selection by shifting the relative importance of different coexistence mechanisms, increasing the importance of fluctuation-dependent mechanisms. For instance, high enrichment might allow consumer-resource oscillations, which might generate coexistence via relative nonlinearity (Armstrong and McGehee 1980; and Appendix D). Note that stronger fluctuating selection with increasing enrichment is not a trivial reflection of larger amplitude fluctuations in species' absolute abundances at high enrichment, because fluctuating selection is associated with fluctuations in relative, not absolute, abundance.

Strong within-year net selection at high enrichment implies that species coexisting in highly enriched lakes must exhibit strong fluctuating selection on among-year timescales, and/or strong trade-offs between competitive ability and resting egg production. Within-year seasonal variation clearly is an important component of plankton dynamics, but our results highlight the need to understand longer term variation as well. Cáceres (1997) found that year-to-year environmental fluctuations promotes the coexistence of *Daphnia galeata mendotae* with *Daphnia pulicaria* via the storage effect. Our results suggest that such fluctuation-dependent coexistence mechanisms may be particularly important contributors to coexistence among the species typical of highly enriched lakes. This hypothesis deserves further study.

Lack of an effect of mean pH on selection arguably is unsurprising. It is unclear why rates of net and fluctuating selection would vary among lakes with different natural pH levels, to which species composition has presumably equilibrated. Analysis of selection in lakes subjected to long-term experimental manipulation of pH would be useful, as would mesocosm experiments manipulating pH while holding species composition constant.

While our results cannot conclusively prove or disprove the operation of fluctuation-dependent coexistence mechanisms, they do argue against the operation

of one large and important class of fluctuation-dependent coexistence mechanisms (i.e., those based on within-year fluctuations in abiotic conditions). Hutchinson (1961) suggested that fluctuating selection might arise from shifts in abiotic conditions that alter species' relative fitnesses. However, fluctuating selection is independent of temporal variability in temperature and pH, suggesting that the substantial variation in fluctuating selection among lake-years is not due to variation in the strength of this "Hutchinsonian" coexistence mechanism. If this "Hutchinsonian" mechanism does vary in strength among lakes, it must arise from fluctuations in abiotic factors independent of the temporal variability of temperature and pH.

Nor does fluctuating selection vary among lake-years because more variable abiotic conditions comprise stronger perturbations to which species exhibit frequency-dependent responses (Appendix D). Several different theoretical models incorporating this mechanism fail to reproduce observed patterns of fluctuating selection along gradients of enrichment and environmental variability (Appendix D). The relatively predictable seasonal succession of plankton species abundances in many lakes implies that species' relative fitnesses do fluctuate in concert with seasonal changes in abiotic variables. Seasonal abiotic variation therefore may set a lower bound on fluctuating selection in natural lakes.

Because our results argue against other candidate sources of fluctuating selection, they strongly suggest an important role for fluctuations in relative abundance generated by species interactions rather than by abiotic variability (e.g., Armstrong and McGehee 1980, Huisman and Weissing 1999, Anderies and Beisner 2000, Abrams et al. 2003). A model incorporating a fluctuation-dependent coexistence mechanism reproduces the observed increase in fluctuating selection with increasing enrichment (Appendix D). An interesting avenue for future theoretical work would be to examine the patterns of net and fluctuating selection predicted by different coexistence mechanisms.

#### *Future directions*

Our statistical approach can help guide and constrain the search for underlying coexistence mechanisms. Any hypothesis about the mechanisms underlying our results must explain why fluctuating selection increases with both natural and experimental enrichment, why net selection increases only with natural enrichment, and why net and fluctuating selection are independent of variability in temperature and pH. We suggest that a productive avenue for future work on coexistence mechanisms will be to estimate the strengths of net and fluctuating selection under both natural and experimentally manipulated conditions (e.g., Nelson et al. 2005). Such work would provide insight into both system dynamics and underlying ecological mechanisms. Such work will need to account for the fact that abiotic and biotic sources of variability can combine in

surprising, nonadditive ways (Reumann et al. 2006), and so their separate effects may not be easily teased apart. Future work should also examine longer time series so as to directly address the hypothesis that longer term fluctuations in relative fitness are crucial for long-term coexistence. Finally, it would be interesting to apply our approach to time series of genotype dynamics (Lynch 1987), thereby obtaining insight into whether plankton species and genetic diversity are maintained via similar mechanisms.

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#### APPENDIX A

Derivation and estimation of selection metrics (*Ecological Archives* E091-119-A1).

#### APPENDIX B

Data summary (*Ecological Archives* E091-119-A2).

#### APPENDIX C

Mesocosm experiment methods (*Ecological Archives* E091-119-A3).

#### APPENDIX D

Selection in simple theoretical models (*Ecological Archives* E091-119-A4).