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Identifying consumer-resource population dynamics using paleoecological data

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ABSTRACT

Ecologists have long been fascinated by cyclic population fluctuations, because they suggest strong interactions between exploiter and victim species. Nonetheless, even for populations showing high-amplitude fluctuations, it is often hard to identify which species are the key drivers of the dynamics, because data are generally only available for a single species. Here, we use a paleoecological approach to investigate fluctuations in the midge population in Lake Mývatn, Iceland, which ranges over several orders of magnitude in irregular, multi-generation cycles. Previous circumstantial evidence points to consumer-resource interactions between midges and their primary food, diatoms, as the cause of these high-amplitude fluctuations. Using a pair of sediment cores from the lake, we reconstructed 26 years of dynamics of midges using egg remains, and algal groups using diagnostic pigments. We analyzed these data using statistical methods that account for both the autocorrelated nature of paleoecological data and measurement error caused by the mixing of sediment layers. The analyses revealed a signature of consumer-resource interactions in the fluctuations of midges and diatoms: diatom abundance (as inferred from biomarker pigment diatoxanthin) increased when midge abundance was low, and midge abundance (inferred from egg capsules) decreased when diatom abundance was low. Similar patterns were not found for pigments characterizing the other dominant algal group in the lake (cyanobacteria), subdominant algae (cryptophytes), or ubiquitous but chemically unstable biomarkers of total algal abundance (chlorophyll-*a*); however, a significant but weaker pattern was found for the chemically stable indicator of total algal populations (β-carotene) to which diatoms are the dominant contributor. These analyses provide the first paleoecological evaluation of specific trophic interactions underlying high amplitude population fluctuations in lakes.

Key words: fossil pigments; Lake Mývatn; Chironomidae; diatoms; population fluctuations; consumer-resource dynamics; Iceland.

INTRODUCTION

Cyclic population dynamics have generated one of the oldest and largest bodies of literature in ecology, starting with the classic models of Lotka showing that population cycles can be generated by predator-prey, or more generally, exploiter-victim interactions (Lotka 1925). Population cycles have generated this interest because they are an easily observed signal of strong interactions among species (Kendall et al. 1999). Despite the numerous population cycles that have been documented, in many cases it is unclear what are the key species driving the cycles. For the iconic snowshoe hare cycles, only extensive research over many decades led to the generally accepted hypothesis that cycles are driven primarily by predation from lynx and other specialist predators, with secondary importance attributed to interactions with the hare food base (Krebs et al. 1995, Krebs 2011). At high latitudes, cycles of microtine rodent populations are common, yet there is still debate over the relative importance of top-down interactions between rodents and predators in driving the cycles (Stenseth 1999, Turchin and Hanski 2001). For insects, numerous cyclic populations have been documented, especially among forest pests; the majority are explained by interactions with predators or parasites, although the identities of the predators or parasites are often just speculations (Myers 1988, Turchin 2003, Turchin et al. 2003, Dwyer et al. 2004). Identifying the interactors who generate cycles between herbivores and plants might be easier given the sedentary nature of plants, but with a few exceptions (Berryman 1976, Berryman et al. 1978), herbivore-plant cycles appear rare. Finally, although there is considerable data on both zooplankton and phytoplankton in lakes, cyclic dynamics that are sustained across multiple years (rather than the well-known annual clear-water period caused by high consumption rates following spring turnover) are apparently rare (Murdoch et al. 1998), despite the ability to find these cycles in the lab (McCauley et al. 1999, McCauley et al. 2008).

68 Thus, understanding most of the population cycles observed in nature is hampered by the absence
69 of data on a candidate partner species.
70 Almost 40 years of ecological monitoring in Lake Mývatn, Iceland, have revealed high-
71 amplitude fluctuations in the abundance of midges (chironomids) that span several orders of
72 magnitude (Einarsson et al. 2002, Einarsson and Gulati 2004, Gardarsson et al. 2004). Because
73 midges make up more than 90% of the secondary production of the lake benthos (1972-1974,
74 Lindegaard and Jónasson 1979), the fluctuations generate huge changes to the trophic structure of
75 the lake and drive fluctuations throughout the lake food web (Einarsson and Gulati 2004). The
76 midge fluctuations are cyclic, in the sense that they show clear, multi-generational peaks and
77 troughs, yet they are not strictly periodic, because the time between consecutive peaks ranges
78 from 4 to 7 years (Gardarsson et al. 2004).
79 Indirect evidence suggests that fluctuations of the dominant midge species, *Tanytarsus*
80 *gracilentus* Holmgren, are driven by resource interactions with their primary food, benthic
81 diatoms and detritus (Ingvason et al. 2004). While almost all of the 20 species of midges in the
82 lake show synchronous population fluctuations, the fluctuations of *T. gracilentus* are the most
83 extreme (5 orders of magnitude) and, at peak abundances, this species makes up roughly 80% of
84 the midge population by numbers (Gardarsson et al. 2004). In the 23-year (46-generation) time
85 series from 1977 to 1999, the adult body size of *T. gracilentus* decreased during the generations
86 before population collapse, suggesting resource limitation leading up to troughs in the cycles
87 (Einarsson et al. 2002). Furthermore, a mathematical model of *T. gracilentus*-diatom-detritus
88 interactions that was fit to time-series data on adult midge fluctuations revealed complex
89 dynamics with alternative states representing either a high-amplitude cycle or a moderately high
90 stable point; the irregular period of midge fluctuations could be explained by the midge
91 population exiting the high-amplitude cycles to spend a stochastic duration of time near the stable

point (Ives et al. 2008). While these empirical and theoretical results support the hypothesis that midge fluctuations arise from consumer-resource interactions within Lake Mývatn, they are based solely on data from fluctuations in adult midges. No information has been available to test whether diatom dynamics are consistent with exploiter-victim cycles.

Here, we use the hindsight offered by paleoecological methods to test whether the dynamics of midges and benthic diatoms could be the result of consumer-resource interactions. Paleoecological approaches are typically used to address ecosystem-level questions, because they provide synoptic information about a system (Smol 2010). This retrospective approach has been used successfully to quantify both algal periodicity (Carpenter and Leavitt 1990) and invertebrate-algal interactions (Leavitt et al. 1989), but never to evaluate the interaction between the two. Here, we combine approaches for the first time, develop novel state-space models to measure reciprocal interactions between herbivores and their resources, and test the population-level hypothesis that fluctuations in diatom and midge abundances are consistent with dynamics expected in tightly coupled consumer-resource interactions. We analyzed two sediment cores from Lake Mývatn representing the period 1975-2003. This time period corresponds closely to our data on midge abundances obtained through trapping adults that began in 1977, and Hauptfleisch et al. (2012) validated the estimates of midge abundances obtained from sedimentary egg counts against the monitoring estimates of adult abundances. From a second core we assayed an array of pigments representing diatoms (diatoxanthin), cyanobacteria that occur in the water column and therefore are not a major component of midge food (echinenone), subdominant cryptophytes (alloxanthin) not heavily consumed by midges, and general indicators of algal abundance that exhibit either robust chemical stability (β-carotene) or are highly labile

(chlorophyll-*a*) (Leavitt and Hodgson 2001). We anticipated that only diatoms would show dynamics consistent with consumer-resource cycles.

To assess the dynamics of midges (egg capsules) and primary producers (pigments), we first analyzed the temporal correlations between these variables. These correlation analyses are complicated by autocorrelation, the tendency of many time series to show correlations between successive samples. Although the complications introduced by autocorrelation are well-known in the statistical and ecological literature, only recently have these complications been acknowledged in the paleoecological literature (Blaauw et al. 2010). We then address the more specific question of whether diatoms increase in abundance when midges are rare and whether midges decrease in abundance when diatoms are rare. The midge population peaks that occur every 4-7 years accentuate the problem of sediment mixing that confronts all paleoecological studies; biotic and abiotic disturbances mix the sediment so that a given stratum contains a mixture of material deposited at different times. This is a form of measurement error that can blur a signal, especially by spreading peaks or filling troughs in the cyclic fluctuations of the variables of interest (Leavitt and Carpenter 1989). Therefore, we developed a statistical method that accounts for sediment mixing to give a more-accurate depiction of population time series from sediment cores. Our overall goal is to show how paleoecological approaches can resurrect historical patterns of population dynamics, provided requisite statistical care is given. In our specific case, we use this approach to give the first direct evidence that consumer-resource interactions could drive the sustained, multi-year fluctuations in midge population dynamics found in Lake Mývatn.

METHODS

Study system

Lake Mývatn is situated in northeastern Iceland at 65°6`N and 17°00`W in an active volcanic area formed by basaltic lava flows (Thorarinsson 1979). Most of the inflow is from groundwater flowing through lava fields, and the resulting high nutrient inputs make the lake highly eutrophic. The maximum natural depth is 4.2 m, with an average depth of 2.5 m. The lake is divided into a north basin (8.5 km^2) and a south basin (28.2 km^2). Water inflow is predominantly from cold and warm springs along the eastern shore. Due to its passage through volcanic basalts, the spring waters contain high concentrations of phosphate (1.62 μM), silica and other dissolved solids, and have a pH ranging between 8.3 and 9.2 (Ólafsson 1979a). The water column is well mixed during the summer months, while thermal stratification and hypoxia occur locally in mid winter (Ólafsson 1979b).

The Icelandic name Mývatn means midge lake after its enormous chironomid swarms. During high-midge years, *T. gracilentus* is by far the most abundant midge species. It has two generations per year, with adults emerging over a 2-3 week period in each of June and late July-August. Gut content analysis of *T. gracilentus* shows a diet of roughly equal parts diatoms and detritus (Ingvason et al. 2004), with much of the detritus likely frass from previous generations and hence coming ultimately from diatoms. Total net primary production for Lake Mývatn in 1972-1973 was about 350 g C/m^2/yr (Jonasson 1979, Jonasson and Adalsteinsson 1979), with most of this from benthic diatoms (220 g C/m^2/yr based on the 1973-1974 silica budget of the lake, Ólafsson 1979a); in 2000-2001, Thorbergsdóttir et al. (2004) estimated total benthic production of 250 and 340 g C/m^2 /yr at two sites using in situ oxygen flux chambers. In addition, extensive lake floor areas of the south basin exhibit loose mats of filamentous green algae (Cladophorales), the extent of which varies greatly on a decadal scale (Einarsson et al. 2004). Blooms of cyanobacteria (*Anabaena spp*.) occur in most years (Jonasson and Adalsteinsson 1979, Einarsson et al. 2004).

Coring and sampling

Two 5-cm diameter sediment cores were retrieved using a Kajak-Brinkhurst corer (Brinkhurst et al. 1969) from 3.75-m deep sites <1 m apart in a sheltered bay, *Breida by Höfdi*, on the east side of Lake Mývatn in June 2006 (Fig. 1). Cores KB-1 and KB-2 were 32- and 34-cm long, respectively, and composed of diatomaceous gyttja (Troels-Smith 1955, Aaby and Berglund 1986), or massive and very moist diatomaceous ooze in the terminology of Schnurrenberger et al. (2003). Core KB-1 was analyzed for loss on ignition (LOI) and arthropod microfossils (cladoceran exuviae and chironomid egg capsules) by Hauptfleisch et al. (2012). Core KB-2 was used for the pigment analysis presented here. The cores were extruded in a vertical position aboard the boat, the outermost 0.5-cm layer of smearing was removed with a spatula, and they were then sliced at 0.5-cm intervals. The samples were placed in plastic bags, sealed and transported in a cooler box immediately to the laboratory on the lakeshore where they were stored at 4°C.

For cores KB-1 and KB-2, we first removed the uppermost 10 cm, as these sediments were highly flocculent and largely uncompacted. The time scale of the cores was fine-tuned by matching the profile of the sediment with known events including documented peaks in chironomid abundances (1979, 1987, 1992, 2000) and a tephra layer from an eruption in Grimsvotn volcano in 2004 (Hauptfleisch et al. 2012). We regressed the time of these events against core depth using a quadratic curve, and all results are subsequently presented in terms of this time scale. The analyzed sections of the cores represent the time period 1975-2004, and the time intervals corresponding to 0.5-cm slices ranged from 0.81 yr at the bottom of the core to 0.30 yr at the top, reflecting compaction of the lower sediments.

To estimate water content and organic matter content, 1 ml of wet sediment was placed in ceramic crucibles and dried at 80°C for 24 h. The dried samples were combusted in a preheated furnace at 550°C for 1 h, cooled in a desiccator for 30 min, and weighed at room temperature (Håkanson and Jansson 1983). For additional background data, diatom proportions (*Fragilaria* spp. vs. non-*Fragilaria* spp.) were counted in the combusted sediment samples.

Pigments

Algal abundance was quantified from fossil pigments and their derivatives. Pigments were extracted from lyophilized (48 h, 0.01 Pa) whole sediment samples, filtered (0.2-μm pore), and dried under pure N_2 gas using the standard methods of Leavitt and Hodgson (2001). Diatoxanthin, echinenone, alloxanthin, β-carotene, and chlorophyll-*a* were isolated and quantified using an Agilent model 1100 high-performance liquid chromatography (HPLC) system equipped with photo-diode array and fluorescence detectors, and calibrated with authentic standards. All pigment concentrations are expressed as nmol pigment/g sediment C, a metric which is linearly correlated to annual algal standing stock in whole-lake calibration studies (reviewed in Leavitt and Hodgson 2001).

Chironomid eggs

We used chironomid eggs as a proxy for chironomids, because they are much more abundant in the sediment and easier to handle than larval head capsules. Egg capsules cannot be identified to species, however, so we cannot separate the different species of midges. For counting, 2 ml of wet sediment were deflocculated by heating in 10% KOH (weight/volume) at 80°C for 2 h and sieved through a 63-µm mesh. The residue was separated by floatation in water

into animal exoskeletal fragments and sand grains. Chironomid egg capsules were identified by their oval, usually slightly asymmetrical shape and smooth surface. The results of the analysis of chironomid egg capsules were published by Hauptfleisch et al. (2012).

Correlations among variables

We first analyzed the correlations among variables through time. Standard statistical tests of the significance of correlations between two variables Y_1 and Y_2 assume that the values of the variable Y_1 are independent of each other, as are the values of Y_2. However, biological processes are often autocorrelated through time; midge and algal abundances might remain at high or low levels for months or years (Einarsson et al. 2004, Gardarsson et al. 2004). Because positive autocorrelation causes a variable of interest to fluctuate slowly over the possible range of values it can take, autocorrelation can increase type I errors (false positives) in statistical tests of correlation between two variables.

To account for possible temporal autocorrelation, we performed the following parametric bootstrap procedure. We first fit an autoregressive-moving average (ARMA) model to each time series. ARMA(p,q) models have the form

$$y(t) - \mu = \sum_{i=1}^{p} \beta_i \left(y(t-1) - \mu \right) + \sum_{j=0}^{q} \alpha_j \varepsilon(t-j) \qquad (1)$$

where $y(t)$ is the value of a variable in sediment stratum t, μ gives the mean of $y(t)$, β_i are the autoregressive coefficients, ε_t is a temporally independent random variable, and α_j are the moving average coefficients (Box et al. 1994, Ives et al. 2010). Thus, the first term on the right-hand side is the autoregressive component of the model, and the second term is the moving average component; the greater the values of p and q, the longer the time lags included in the AR and MA

components of the model. ARMA models are flexible enough to fit potentially complex patterns of autocorrelation (Ives et al. 2010), and we used Akaike's Information Criterion corrected for small sample sizes (AICc) to select the values of p and q that give the best fits to the time series. We then simulated data from the best-fitting ARMA models and computed pairwise Pearson's correlation coefficients from the simulated data sets. Repeating this for 100,000 simulated data sets gives the approximate distribution of the estimator (Efron and Tibshirani 1993) of the correlation coefficient under the null hypothesis that the time series $y_1(t)$ and $y_2(t)$ are independent but temporally autocorrelated, and we used this to compute p-values. Because we were interested in fluctuations in the response variables, we detrended the response variables with a quadratic function, $y(t) = c_0 + c_1 t + c_2 t^2$, and standardized the residuals to have standard deviation 1 (Patoine and Leavitt 2006). This removes possible degradation or transformation of pigments through time.

When considering correlations among several variables, we also used the bootstrap procedure to obtain p-values corrected for multiple comparisons using an approach comparable to a sequential (Holm) Bonferroni correction (Holm 1979). We first ordered the K correlation coefficients from lowest to highest p-value. For the first correlation coefficient, we counted the proportion of simulated data sets (including all variables) for which one or more of the K correlation coefficients had a lower p-value; this proportion gives the corrected p-value for the first correlation coefficient. We then excluded this correlation coefficient from the simulated data sets and repeated the procedure for the second correlation coefficient, asking what proportion of the simulated data sets had one or more of the $K - 1$ p-values lower than the observed p-value of the second correlation coefficient. We repeated this procedure, excluding correlation coefficients until the corrected p-value exceeded 0.05. This approach allowed us to report p-values that account for the multiple correlation coefficients we computed.

State-space model

Whereas our parametric bootstrap procedure gives a statistically valid method for assessing correlations among variables, we also wanted to test the more-mechanistic hypothesis that high midge abundance (egg capsules) caused diatom abundance (diatoxanthin) to decrease, while high diatom abundance allowed midges to increase. For this we designed a state-space model (Harvey 1989) that explicitly incorporates both autocorrelation and measurement error generated by sediment mixing. We performed analyses not only for diatoxanthin, but also for echinenone, alloxanthin, β-carotene, and chlorophyll-*a*; we expected the strongest interaction between midges and diatoms, so these other pigments serve as statistical controls. Note, however, that they are not independent; for example, diatoms contain not only diatoxanthin but also β-carotene and chlorophyll-*a*. Differences in chemical stability of the latter two pigments allowed us to evaluate whether our approach was additionally subject to diagenetic effects of post-depositional pigment degradation. As reviewed in Leavitt and Hodgson (2001), the carotenoids used in this study are all well preserved in lake sediments, in contrast to ubiquitous chlorophyll-*a* which is rapidly transformed or discolored in surface deposits.

The state-space model comprises two sets of equations, one describing process error (biological variability) and the other measurement error (including vertical mixing of sediment). The process equations are

$$\begin{aligned} \log x_1(t) &= b_{10} + \tau(t)\left[b_{11}\left(\log x_1(t-1) - b_{10}\right) + b_{12}\log x_2(t-1)\right] + \varepsilon_1(t) \\ \log x_2(t) &= b_{20} + \tau(t)\left[b_{22}\left(\log x_2(t-1) - b_{20}\right) + b_{21}\log x_1(t-1)\right] + \varepsilon_2(t) \end{aligned}, \qquad (2)$$

where $\log x_1(t)$ is the natural logarithm of the concentration of the algal pigment of interest, and $\log x_2(t)$ is log midge egg capsule abundance. We modeled variables on a log scale because we

expect ecological processes to act multiplicatively; taking the log allows the use of a linear autoregressive model and is formally equivalent to a Gompertz multiplicative population model (Dennis and Taper 1994). The samples t give the consecutive 0.5-cm core slices rescaled to time in years (see *Methods: Coring and sampling*). To account for sediment compaction, $\tau(t)$ gives the time interval between the core samples at t–1 and t. The Gaussian random variables $\varepsilon_i(t)$ with means zero and variances σ^2_i represent variation in log $x_i(t)$ between samples. The coefficients b_{i0} give the expected value of log $x_i(t)$, b_{ii} measures the autocorrelation of log $x_i(t)$ from one sample to the next, and b_{ij} measures the effect of log $x_j(t)$ on log $x_i(t)$; thus, if b_{12} is negative, then high midge abundances are associated with decreases in log pigment concentration between samples t and $t + 1$, and if b_{21} is positive, then high pigment concentrations are associated with increases in log midge egg capsules.

The measurement equations are

$$x_1(t)^* = \sum_{T=0}^{r} a^T x(t-T) + \phi_1(t)$$

$$x_2(t)^* = \sum_{T=0}^{r} a^T u(t-T) + \phi_2(t) \qquad (3)$$

where $x_1(t)^*$ and $x_2(t)^*$ are the observed values of $x_1(t)$ and $x_2(t)$ at time t. Because mixing of sediment is an additive process, the measurement equations are formulated using the untransformed values of $x_1(t)$ and $x_2(t)$. To account for sediment mixing, the observed values $x_1(t)^*$ and $x_2(t)^*$ depend not only on the sedimentation rates of $x_1(t)$ and $x_2(t)$ at sample t, but also on the sedimentation for r core increments into the past (lower sediments). The sedimentation rates T time steps in the past are discounted by the term a^T ($a < 1$), so that spatially more-distant sediments have lower mixing with the sediments in sample t. This equation makes the simplifying approximation that the sediments in sample t are mixed with lower sediments but not

297 with sediments above; while this is the case immediately following the deposition of sediment,
298 later mixing with higher sediments will occur (Leavitt and Carpenter 1989). We address this
299 asymmetry in more detail with simulations in Appendix A (online Supplemental Material).
300 Finally, $\phi_1(t)$ and $\phi_2(t)$ are Gaussian random variables with variances $x_1(t)\upsilon^2_1$ and $x_2(t)\upsilon^2_2$. These
301 variances are proportional to the mean under the assumption that sampling variability is
302 approximately Poisson; this also prohibits negative values of $x_1(t)^*$ and $x_2(t)^*$ when the predicted
303 values of $x_1(t)$ and $x_2(t)$ are small. Because separate cores were taken for algal pigments and
304 midge egg capsules, we assumed zero correlation between $\phi_1(t)$ and $\phi_2(t)$.
305 We fit the state-space model given by equations 2 and 3 using an extended Kalman filter
306 to calculate the likelihood function (Harvey 1989). Maximum likelihood parameter values were
307 estimated for 11 variables: b_{10}, b_{20}, b_{12}, b_{21}, b_{11}, b_{22}, a, σ^2_1, σ^2_2, υ^2_1, and υ^2_2. We tested the
308 statistical significance of the effect of midge abundance on pigments, b_{12}, and pigments on midge
309 abundance, b_{21}, using likelihood ratio tests to compare the full 11-parameter model with the
310 reduced 9-parameter model in which $b_{12} = b_{21} = 0$, as well as the separate 10-parameter models
311 with either $b_{12} = 0$ or $b_{21} = 0$. Likelihood ratio tests are based on the asymptotic approximation
312 that with large sample sizes, the log-likelihood ratios are χ^2 distributed with degrees of freedom
313 equal to the difference in the number of parameters between models (Harvey 1989). We
314 performed these analyses for $r = 3$ which sets the maximum mixing distance at 3 core sections (2
315 cm). To account for possible trends in variables through time, we first quadratically detrended all
316 variables. After detrending, we added a constant to each time series to give it the same minimum
317 value as the non-detrended time series, and then standardized to give each time series a variance
318 of one. For fitting the model, we assumed that the initial values of $x_i(0)$ were their observed
319 values. The initial variances of $\log x_1(0)$ and $\log x_2(0)$ were set to σ^2_1 and σ^2_2, with zero

covariance. Our statistical approach allows direct evaluation of whether the dynamics of midges and algae observed in the sediment are consistent with strong consumer-resource interactions.

Validation using a simulation model

Because the midge dynamics inferred from adult data are not strictly periodic, we tested whether the state-space approach (Eqs. 2, 3) could detect negative effects of midges on diatoms and positive effects of diatoms on midges even for non-periodic data that we would expect in Lake Mývatn. We generated simulated core data by predicting midge and diatom abundances from the midge-diatom-detritus model that we previously fit to the adult midge time series (Ives et al. 2008); this model showed possible alternative states underlying *Tanytarsus gracilentus* dynamics. Using the model to generate midge and diatom abundances, we then simulated the sedimentation process including both deposition and mixing between adjacent sediment layers; details are giving in Appendix A (online Supplemental Material). We fit the simulated data using the same procedure as we used for the real sediment core data. If the model fit to simulated data gives similar results to those when fit to the real data, then we can be confident that our approach will detect consumer-resource interactions even when these interactions do not lead to cycles with regular periods.

RESULTS

Our analyses focus on the interactions between midge abundance (egg capsules) and the abundances of diatoms (diatoxanthin), cyanobacteria (echinenone), cryptophytes (alloxanthin), and total algal abundance as recorded by chemically stable (β-carotene) and labile biomarkers (chlorophyll-*a*) (Appendix B, Fig. B1). As expected, the strongest correlations were recorded

between the two markers of total algal abundance, as well as total algal abundance and the predominant benthic (diatom) and planktonic (cyanobacteria) algal groups (Table 1). Weaker correlations were observed between planktonic cyanobacteria (echinenone) and cryptophytes (alloxanthin). In contrast, only concentrations of the pigment diatoxanthin (diatoms) were correlated significantly (–0.37) with midge egg capsules (Table 1).

Statistical significance of these correlations (Table 1) was determined by parametric bootstrapping to account for autocorrelation in the individual time series. We also computed p-values using standard Pearson correlation coefficients (Table 2). In all cases the p-values ignoring autocorrelation were smaller than those computed when accounting for autocorrelation; for example, the standard p-value for the correlation of –0.37 between midge egg capsules and diatoxanthin was 0.012, whereas the bootstrap estimate was 0.039. This comparison underscores the need to account for autocorrelation when comparing fossil time series.

Diatoxanthin showed peaks in 1977, 1983, 1987, and 1999 that preceded peaks in midge egg capsule counts (Fig. 2). This pattern is consistent with consumer-resource interactions in which increases in diatoms occur at low midge abundance, and increases in midges occur at high diatom abundance. In the state-space model (Eqs. 2, 3) the estimate for the effect of midges on diatoxanthin is $b_{12} = –0.90$, and the effect of diatoxanthin on midges is $b_{21} = 0.46$ (Table 3); both of these coefficients are significantly different from zero separately (b_{12}: $\chi^2_1 = 13.08$, P = 0.0003; b_{21}: $\chi^2_1 = 6.46$, P = 0.011) and together ($\chi^2_2 = 26.84$, P < 0.0001). In addition, the analysis of midge egg capsules and β-carotene gave a negative estimate of $b_{12} = –0.54$ ($\chi^2_1 = 9.79$, P = 0.0017) and a positive estimate of $b_{21} = 0.33$ ($\chi^2_1 = 4.04$, P = 0.044), similar to but weaker than the interactions inferred between midges and diatoxanthin. None of the other pigments showed statistically significant values of b_{12} and b_{21}, suggesting that the associated algae were not

366 involved in consumer-resource cycles (Table 3). Furthermore, the absence of significant
367 estimates if b_{12} and b_{21} for ubiquitous chlorophyll *a* confirms that models can be influenced by
368 post-depositional degradation of fossil records.

369 The state-space model fit to midge egg capsules and diatoxanthin gives information not
370 only about interaction strengths b_{12} and b_{21}, but also about other properties inferred from the data.
371 The best-fitting state-space model (Table 3) gave an estimate of $a = 0.55$ ($\chi^2_1 = 9.13$, P = 0.0025).
372 This value of *a* implies that 0.50 of the diatoxanthin remained in the sediment stratum where it
373 was deposited, while 0.27 ($= a/(1+a+a^2+a^3)$, 0.15, ($= a^2/(1+a+a^2+a^3)$ and 0.08 ($= a^3/(1+a+a^2+a^3)$
374 represent sediment from slices 0.5, 1.0, and 1.5 cm below the observed core slice. This value of *a*
375 is similar for other pigments, except for the lower value estimated for echinenone. The fitted
376 value of b_{11} is close to zero, implying that there is little autocorrelation in diatom abundances
377 through time that is not explained by midge abundance; in contrast, $b_{22} = 1.29$, implying strong
378 autocorrelation in midge abundance. In contrast to these model parameters, other model
379 parameters were not informative. Specifically, the magnitudes of the process and sampling errors
380 (σ^2_i and υ^2_i) often traded off against each other, so that $\sigma^2_i > 0$ and $\upsilon^2_i = 0$, or $\sigma^2_i = 0$ and $\upsilon^2_i > 0$.
381 This is the result of the difficulty of statistically separating process error from measurement error.

382 To validate the state-space modeling approach, we simulated midge and diatom
383 abundance data using the model that had been fit to adult *T. gracilentus* data collected during
384 1977-2002 (Ives et al. 2008), and then simulated the sedimentation process including mixing
385 among layers (Appendix A). As we found for the real core data, the analysis of the simulated core
386 data identified a negative value of $b_{12} = –0.55$ and positive value of $b_{21} = 0.82$, both of which
387 were statistically significant. The simulations show that the state-space model (Eq. 2 and 3) is

388 robust to pronounced but complex (aperiodic) variation in population abundance caused by
389 consumer-resource interactions.
390
391 ## DISCUSSION
392 Paleoecological analysis of fossil midges (egg capsules) and diatoms (diatoxanthin)
393 provided direct support for the hypothesis that the dramatic midge population fluctuations in
394 Lake Mývatn are driven mainly by consumer-resource interactions between midges and their
395 food. Our state-space model showed that high midge egg capsule densities were associated with
396 decreases in diatoxanthin concentration and, in turn, high diatoxanthin concentrations were
397 associated with increases in midges. Furthermore, β-carotene (algae) showed a similar though
398 weaker pattern, consistent with the fact that diatoms are a main component of the algal
399 assemblage, and that changes in concentration of diatoxanthin and β-carotene were highly
400 correlated (Table 1). In contrast, none of other pigments showed significant correlation with
401 midge abundance.
402 Although concomitant changes in diatoms and midges do not prove that consumer-
403 resource interactions underlie the observed decadal-scale population fluctuations, several lines of
404 evidence suggest that population fluctuations are not driven by other trophic interactions within
405 Lake Mývatn. Two other general possibilities are bottom-up effects on diatoms (i.e., some other
406 interaction drives diatom fluctuations, and midges follow) and top-down effects on midges (i.e.,
407 some other interaction drives midge fluctuations, and diatoms follow). For the bottom-up
408 alternative, there would have to be a driver of diatom fluctuations other than midges. Diatoms are
409 the dominant group of primary producers in the lake, accounting for over 50% of primary
410 production (see *Methods: Study system*). Furthermore, most primary production is benthic rather

411 than pelagic, and diatoms are the dominant benthic primary producers (>95% of them are benthic
412 Fragilariaceae spp., Einarsson 1982). Thus, if there were an as yet unidentified driver of diatom
413 fluctuations, this driver would have to be strong enough to cause large fluctuations in benthic
414 primary production. Possible candidates for strong drivers are the mainly pelagic herbivore,
415 *Daphnia longispina*, and the epibenthic large-bodied cladocerans, and these do fluctuate in
416 synchrony with midges (Einarsson and Örnólfsdóttir 2004). Nonetheless, midges perform more
417 than 80% of the secondary production in the benthos (Lindegaard and Jónasson 1979), and
418 therefore are much better candidates for drivers of diatom abundance. Another possible candidate
419 for a driver of diatom fluctuations is *Anabaena* spp. that limit the growth of diatoms via shading.
420 Nonetheless, in the core data *Anabaena* spp. (as measured by echinenone) fluctuate in synchrony
421 with diatoms (diatoxanthin) (Table 1), which argues against shading from *Anabaena* spp. driving
422 diatom fluctuations.

423 The second general alternative hypothesis is that top-down forces generate fluctuations in
424 midges, and diatoms fluctuate in response. The obvious candidate for a top-down driver of midge
425 fluctuations is stickleback fish. Gut content analyses show that sticklebacks consume midges,
426 with midges comprising up to 56% of gut contents in a high-midge year and 9% in a low-midge
427 year (Gíslason et al. 1998). Nonetheless, the dominant midge, *T. gracilentus*, is better protected
428 than other midge species in their heavily constructed tubes and seems to be avoided by
429 sticklebacks. Furthermore, analyses of the time series of midges and sticklebacks (Einarsson et al.
430 2002) did not show the out-of-phase fluctuations that is expected for predator-prey cycles, instead
431 suggesting that sticklebacks follow rather than drive midge fluctuations. In addition to predators,
432 it is also possible that there is an unidentified parasite or pathogen that drives midge population
433 fluctuations, although we have little evidence for this.

434 Historical changes in grazing intensity and lake hydrology do not appear to have biased

435 the formation of the fossil record, nor the reliability of sedimentary time series as metrics of past
436 population abundance. Although intensification of herbivory is known to increase the rates of
437 deposition of algae and their pigments (Leavitt and Carpenter 1990), empirical (Leavitt et al.
438 1989) and modeling evidence (Cuddington and Leavitt 1999) show that this effect is limited to
439 less than a year in duration. Similarly, ecosystem-scale nutrient mass budgets reveal that over
440 90% of inflow silica is retained in the lake (Ólafsson 1979a), mainly due to uptake by and
441 deposition in diatoms (Opfergelt et al. 2011).
442
443 *Statistical Methods*
444 We developed a bootstrap method for determining the statistical significance of
445 correlations between two time series when each has temporal autocorrelation. Comparing its
446 results to standard correlations (Table 2) shows that standard correlations are likely to generate
447 type I errors (false positives). This can be explained simply with an example. Suppose there are
448 two 100-year time series that both show cycles with strict 10-year periods yet are independent.
449 There is a 20% chance that they fluctuate in either perfect synchrony or perfect asynchrony
450 (lagged by 5 years) for 100 years, which would clearly show very high statistical significance in a
451 standard correlation test; even if they were lagged by 1 or 6 years, the standard correlations
452 would likely be significant. Thus, it would be easy to get statistically significant correlations even
453 though we know that the time series are independent. Our bootstrap approach corrects for
454 autocorrelation and hence does not suffer from this potential source of type I errors.
455 Our state-space model takes a more-mechanistic approach, modeling explicit interactions
456 between variables and incorporating measurement error that accounts for sediment mixing. The
457 mathematical description of sediment mixing is simplistic, assuming that sediment layers below a
458 given strata have an influence that tapers off geometrically with depth. This is similar to the

assumption used by Blaauw and Christen (2011) to construct a model relating sediment depth to age determined by radiocarbon dating. Nonetheless, there are numerous bioturbation (Kristensen et al. 2012) models that incorporate much more sophisticated assumptions about the physical and biological processes underlying sediment mixing (Sandnes et al. 2000, Meysman et al. 2005, Schiffers et al. 2011). We have not attempted to incorporate the complexities of bioturbation into our model, because the information needed to apply these approaches is unknown for our system. Therefore, our approach matches the level of detail in the model to the data we have. When applied to simulated data (Appendix A, online Supplemental Material), the approach did identify the effects of sedimentation in smoothing the fluctuations in deposition rates. Despite this smoothing effect, the state-space model still identified strong interactions between midges and diatoms in both simulated and real data.

Conclusion

Our analyses of sediment core data give strong support to the midge-diatom consumer-resource hypothesis to explain the fluctuations in midge and diatom abundances in Lake Mývatn. Sediment cores are the only source of information about diatom fluctuations in Lake Mývatn, because continuous long-term monitoring was not performed. Our example thus illustrates the benefits of paleoecology to reconstruct history and extract missing information that is preserved in sediment cores. This information is not limited to broad, ecosystem-level processes, but can also be used to understand the population dynamical interactions between species.

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621

622 APPENDIX A

623 Simulation of midge and diatom abundance data.

624

625 APPENDIX B

626 Stratigraphy of pigments, loss on ignition (LOI), C, N, $\delta^{13}C$, diatoms, chironomid eggs and

627 Cladocera exuviae in the sediment cores.

628

Table 1: Correlations among six variables from two sediment cores.

	Midge eggs	Dia	Echin	Allox	β-caro
Diatoxanthin	-0.37*				
Echinenone	-0.16	0.42*			
Alloxanthin	-0.03	0.25	0.34*		
β-carotene	-0.19	0.64**††	0.52**	–0.01	
Chlorophyll-*a*	0.09	0.53*	0.53*	0.17	0.77**††

* $P < 0.05$, ** $P < 0.01$, calculated from a bootstrap that incorporates autocorrelation (Eq. 1)

† $P < 0.05$, †† $P < 0.01$, calculated from a bootstrap Holm-Bonferroni correct for multiple comparisons that incorporates autocorrelation (Eq. 1)

636 Table 2: P-values (2-tailed and not corrected for multiple comparisons) from a standard Pearson
637 correlation test (upper-right triangle) and from the bootstrap (Eq. 1) that accounts for temporal
638 autocorrelation (lower-left triangle).

	Midge eggs	Dia	Echin	Allox	β-caro	Chl-*a*
Midge eggs		0.012	0.29	0.87	0.20	0.52
Diatoxanthin	0.039		0.002	0.08	0.0000	0.0000
Echinenone	0.35	0.018		0.016	0.0001	0.0000
Alloxanthin	0.88	0.19	0.046		0.98	0.23
β-carotene	0.27	0.0001	0.003	0.96		0.0000
Chlorophyll-*a*	0.67	0.011	0.011	0.43	0.0003	

639

640 Table 3: Parameter estimates from the state-space model given by equations 2 and 3 for each of

641 five pigments.

Coefficient	Diatoxanthin	Echinenone	Alloxanthin	βcarotene	Chl-*a*
b_{11}	-0.10	1.54	0.65	1.21	1.81
b_{22}	1.29	0.40	0.11	1.42	0.09
b_{12}	-0.90***	0.00	-0.10	-0.54**	-0.04
b_{21}	0.46*	-0.24	-0.31***	0.33*	0.65
b_{10}	0.36	0.75	0.21	0.32	0.89
b_{20}	-0.03	0.33	-0.08	-0.03	0.06
a	0.55	0.21	0.44	0.48	0.46
σ_1	0.39	0.00	0.38	0.00	0.00
σ_2	0.00	0.53	0.60	0.00	0.65
υ_1	0.00	-0.40	0.29	0.35	-0.17
υ_2	0.49	0.00	0.08	0.52	0.00
LL	-70.87	-79.76	-72.81	-73.68	-59.56
LRT χ^2_2	26.84	0.14	17.60	17.89	4.52
p-value	<0.0001	0.93	0.0002	<0.0001	0.10

642 *P < 0.05, **P < 0.01, ***P < 0.001

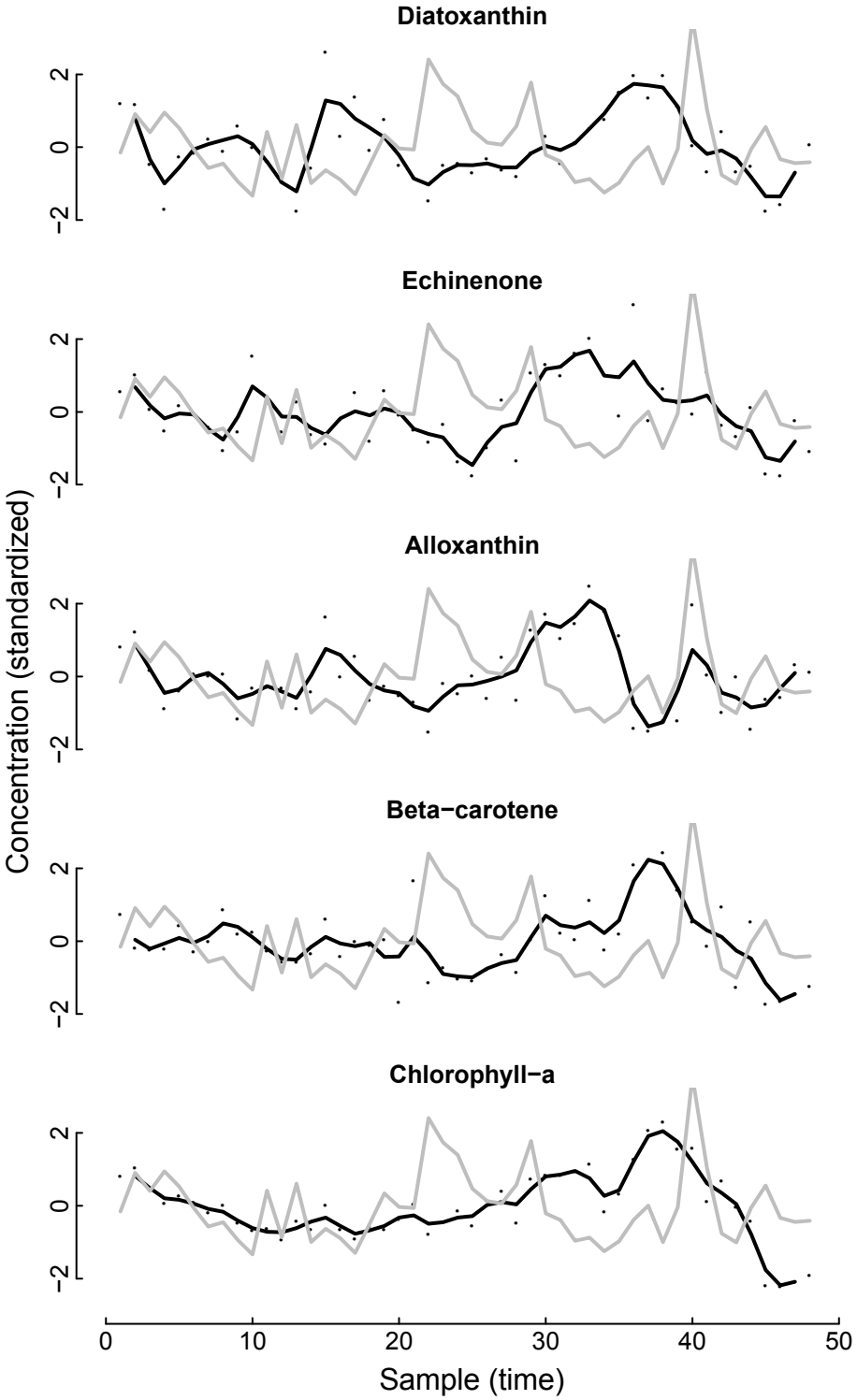
643

644

645 Fig. 1: Detrended sediment core data for midge egg capsules and diatoxanthin, echinenone,
646 alloxanthin, β-carotene, and chlorophyll-*a* (dots). Smoothing of midge (gray lines) and pigment
647 data (black lines) was performed to make fluctuating patterns in the data more clear; a direct form
648 II transposed filter was used with numerator coefficients (0.25, 0.5, 0.25), and denominator
649 coefficient 1.

650

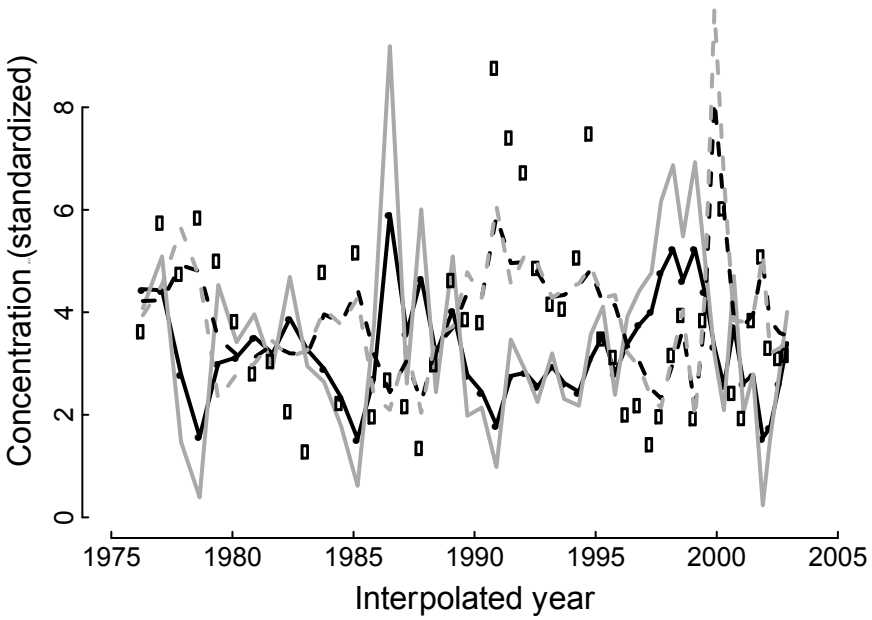
651 Fig. 2: Fit of the state-space model (Eqs. 2, 3) to detrended diatoxanthin (solid dots) and midge
652 egg capsule abundance (open dots). Solid and dashed black lines give the fit of the model to the
653 observed values $x^*(t)$ and $u^*(t)$ of diatoxanthin and midges (Eq. 3), whereas the solid and dashed
654 gray lines give the estimates of the deposition rates prior to sediment mixing (Eq. 2).


Diatoxanthin
Echinenone
Alloxanthin
Beta−carotene
Chlorophyll−a
Concentration (standardized)
Sample (time)
−2
0
2
0
10
20
30
40
50

655

656

657


Concentration (standardized)
0
2
4
6
8
1975
1980
1985
1990
1995
2000
2005
Interpolated year

658

659

660