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1 **Identifying consumer-resource population dynamics using paleoecological data**

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19 ABSTRACT

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

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

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## INTRODUCTION

45  
46           Cyclic population dynamics have generated one of the oldest and largest bodies of  
47 literature in ecology, starting with the classic models of Lotka showing that population cycles can  
48 be generated by predator-prey, or more generally, exploiter-victim interactions (Lotka 1925).  
49 Population cycles have generated this interest because they are an easily observed signal of  
50 strong interactions among species (Kendall et al. 1999). Despite the numerous population cycles  
51 that have been documented, in many cases it is unclear what are the key species driving the  
52 cycles. For the iconic snowshoe hare cycles, only extensive research over many decades led to  
53 the generally accepted hypothesis that cycles are driven primarily by predation from lynx and  
54 other specialist predators, with secondary importance attributed to interactions with the hare food  
55 base (Krebs et al. 1995, Krebs 2011). At high latitudes, cycles of microtine rodent populations  
56 are common, yet there is still debate over the relative importance of top-down interactions  
57 between rodents and predators in driving the cycles (Stenseth 1999, Turchin and Hanski 2001).  
58 For insects, numerous cyclic populations have been documented, especially among forest pests;  
59 the majority are explained by interactions with predators or parasites, although the identities of  
60 the predators or parasites are often just speculations (Myers 1988, Turchin 2003, Turchin et al.  
61 2003, Dwyer et al. 2004). Identifying the interactors who generate cycles between herbivores and  
62 plants might be easier given the sedentary nature of plants, but with a few exceptions (Berryman  
63 1976, Berryman et al. 1978), herbivore-plant cycles appear rare. Finally, although there is  
64 considerable data on both zooplankton and phytoplankton in lakes, cyclic dynamics that are  
65 sustained across multiple years (rather than the well-known annual clear-water period caused by  
66 high consumption rates following spring turnover) are apparently rare (Murdoch et al. 1998),  
67 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

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

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

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

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

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## METHODS

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### *Study system*



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

148 The Icelandic name Mývatn means midge lake after its enormous chironomid swarms.  
149 During high-midge years, *T. gracilentus* is by far the most abundant midge species. It has two  
150 generations per year, with adults emerging over a 2-3 week period in each of June and late July-  
151 August. Gut content analysis of *T. gracilentus* shows a diet of roughly equal parts diatoms and  
152 detritus (Ingvason et al. 2004), with much of the detritus likely frass from previous generations  
153 and hence coming ultimately from diatoms. Total net primary production for Lake Mývatn in  
154 1972-1973 was about 350 g C/m<sup>2</sup>/yr (Jonasson 1979, Jonasson and Adalsteinsson 1979), with  
155 most of this from benthic diatoms (220 g C/m<sup>2</sup>/yr based on the 1973-1974 silica budget of the  
156 lake, Ólafsson 1979a); in 2000-2001, Thorbergsdóttir et al. (2004) estimated total benthic  
157 production of 250 and 340 g C/m<sup>2</sup>/yr at two sites using in situ oxygen flux chambers. In addition,  
158 extensive lake floor areas of the south basin exhibit loose mats of filamentous green algae  
159 (Cladophorales), the extent of which varies greatly on a decadal scale (Einarsson et al. 2004).  
160 Blooms of cyanobacteria (*Anabaena spp.*) occur in most years (Jonasson and Adalsteinsson 1979,  
161 Einarsson et al. 2004).

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### *Coring and sampling*

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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 Höfði*, 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.

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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.

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

190

### 191 *Pigments*

192 Algal abundance was quantified from fossil pigments and their derivatives. Pigments  
193 were extracted from lyophilized (48 h, 0.01 Pa) whole sediment samples, filtered (0.2- $\mu$ m pore),  
194 and dried under pure N<sub>2</sub> gas using the standard methods of Leavitt and Hodgson (2001).  
195 Diatoxanthin, echinenone, alloxanthin,  $\beta$ -carotene, and chlorophyll-*a* were isolated and  
196 quantified using an Agilent model 1100 high-performance liquid chromatography (HPLC)  
197 system equipped with photo-diode array and fluorescence detectors, and calibrated with authentic  
198 standards. All pigment concentrations are expressed as nmol pigment/g sediment C, a metric  
199 which is linearly correlated to annual algal standing stock in whole-lake calibration studies  
200 (reviewed in Leavitt and Hodgson 2001).

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### 202 *Chironomid eggs*

203 We used chironomid eggs as a proxy for chironomids, because they are much more  
204 abundant in the sediment and easier to handle than larval head capsules. Egg capsules cannot be  
205 identified to species, however, so we cannot separate the different species of midges. For  
206 counting, 2 ml of wet sediment were deflocculated by heating in 10% KOH (weight/volume) at  
207 80°C for 2 h and sieved through a 63- $\mu$ m mesh. The residue was separated by floatation in water

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

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### 212 *Correlations among variables*

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

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

$$224 \quad y(t) - \mu = \sum_{i=1}^p \beta_i (y(t-1) - \mu) + \sum_{j=0}^q \alpha_j \varepsilon(t-j) \quad (1)$$

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

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

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

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*State-space model*

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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,  $\beta$ -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  $\beta$ -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

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

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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

276 expect ecological processes to act multiplicatively; taking the log allows the use of a linear  
 277 autoregressive model and is formally equivalent to a Gompertz multiplicative population model  
 278 (Dennis and Taper 1994). The samples  $t$  give the consecutive 0.5-cm core slices rescaled to time  
 279 in years (see *Methods: Coring and sampling*). To account for sediment compaction,  $\tau(t)$  gives the  
 280 time interval between the core samples at  $t-1$  and  $t$ . The Gaussian random variables  $\varepsilon_i(t)$  with  
 281 means zero and variances  $\sigma_i^2$  represent variation in  $\log x_i(t)$  between samples. The coefficients  $b_{i0}$   
 282 give the expected value of  $\log x_i(t)$ ,  $b_{ii}$  measures the autocorrelation of  $\log x_i(t)$  from one sample  
 283 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  
 284 midge abundances are associated with decreases in log pigment concentration between samples  $t$   
 285 and  $t + 1$ , and if  $b_{21}$  is positive, then high pigment concentrations are associated with increases in  
 286 log midge egg capsules.

287 The measurement equations are

$$\begin{aligned}
 x_1(t)^* &= \sum_{T=0}^r a^T x(t-T) + \phi_1(t) \\
 x_2(t)^* &= \sum_{T=0}^r a^T u(t-T) + \phi_2(t)
 \end{aligned}
 \tag{3}$$

289 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  
 290 sediment is an additive process, the measurement equations are formulated using the  
 291 untransformed values of  $x_1(t)$  and  $x_2(t)$ . To account for sediment mixing, the observed values  
 292  $x_1(t)^*$  and  $x_2(t)^*$  depend not only on the sedimentation rates of  $x_1(t)$  and  $x_2(t)$  at sample  $t$ , but also  
 293 on the sedimentation for  $r$  core increments into the past (lower sediments). The sedimentation  
 294 rates  $T$  time steps in the past are discounted by the term  $a^T$  ( $a < 1$ ), so that spatially more-distant  
 295 sediments have lower mixing with the sediments in sample  $t$ . This equation makes the  
 296 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  $x_1(t)v_1^2$  and  $x_2(t)v_2^2$ . 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:  $b_{10}$ ,  $b_{20}$ ,  $b_{12}$ ,  $b_{21}$ ,  $b_{11}$ ,  $b_{22}$ ,  $a$ ,  $\sigma_1^2$ ,  $\sigma_2^2$ ,  $v_1^2$ , and  $v_2^2$ . 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  $\chi^2$  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  $\sigma_1^2$  and  $\sigma_2^2$ , with zero



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

322

### 323 *Validation using a simulation model*

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

337

## 338 RESULTS

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

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

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

355 Diatoxanthin showed peaks in 1977, 1983, 1987, and 1999 that preceded peaks in midge  
356 egg capsule counts (Fig. 2). This pattern is consistent with consumer-resource interactions in  
357 which increases in diatoms occur at low midge abundance, and increases in midges occur at high  
358 diatom abundance. In the state-space model (Eqs. 2, 3) the estimate for the effect of midges on  
359 diatoxanthin is  $b_{12} = -0.90$ , and the effect of diatoxanthin on midges is  $b_{21} = 0.46$  (Table 3); both  
360 of these coefficients are significantly different from zero separately ( $b_{12}$ :  $\chi^2_1 = 13.08$ ,  $P = 0.0003$ ;  
361  $b_{21}$ :  $\chi^2_1 = 6.46$ ,  $P = 0.011$ ) and together ( $\chi^2_2 = 26.84$ ,  $P < 0.0001$ ). In addition, the analysis of  
362 midge egg capsules and  $\beta$ -carotene gave a negative estimate of  $b_{12} = -0.54$  ( $\chi^2_1 = 9.79$ ,  $P =$   
363  $0.0017$ ) and a positive estimate of  $b_{21} = 0.33$  ( $\chi^2_1 = 4.04$ ,  $P = 0.044$ ), similar to but weaker than  
364 the interactions inferred between midges and diatoxanthin. None of the other pigments showed  
365 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 ( $\sigma^2_i$  and  $\upsilon^2_i$ ) 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 Paleocological 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,  $\beta$ -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  $\beta$ -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 Örnólfssdóttir 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

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

470

#### 471 *Conclusion*

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

479

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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,  $\delta^{13}\text{C}$ , diatoms, chironomid eggs and

627 Cladocera exuviae in the sediment cores.

628

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

	Midge				
	eggs	Dia	Echin	Allox	$\beta$ -caro
Diatoxanthin	-0.37*				
Echinenone	-0.16	0.42*			
Alloxanthin	-0.03	0.25	0.34*		
$\beta$ -carotene	-0.19	0.64**††	0.52**	-0.01	
Chlorophyll- <i>a</i>	0.09	0.53*	0.53*	0.17	0.77**††

630  
 631 \*  $P < 0.05$ , \*\*  $P < 0.01$ , calculated from a bootstrap that incorporates autocorrelation (Eq. 1)

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

634

635

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	$\beta$ -caro	Chl- <i>a</i>
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
$\beta$ -carotene	0.27	0.0001	0.003	0.96		0.0000
Chlorophyll- <i>a</i>	0.67	0.011	0.011	0.43	0.0003	

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

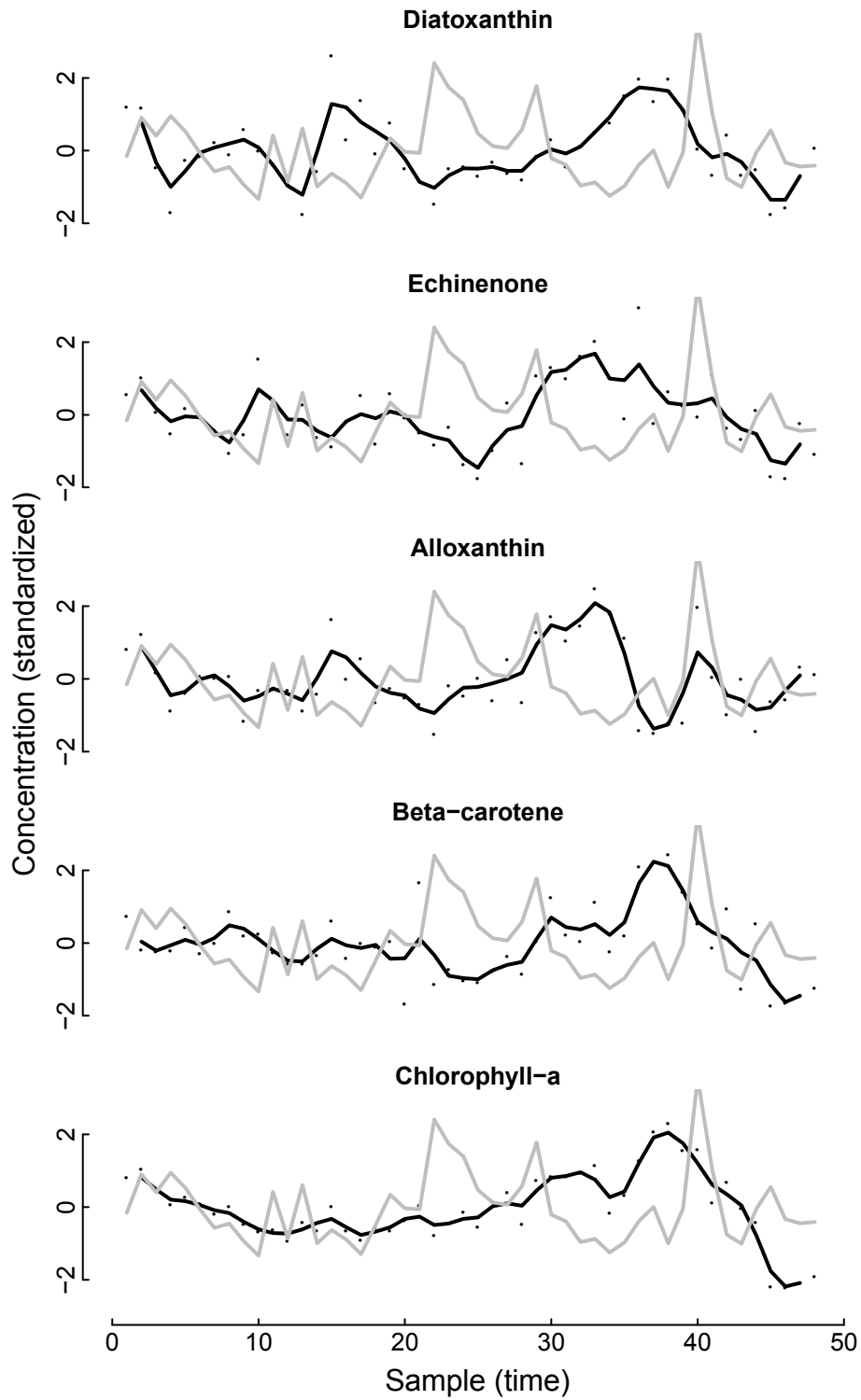
Coefficient	Diatoxanthin	Echinenone	Alloxanthin	$\tilde{\beta}$ carotene	Chl- <i>a</i>
$b_{11}$	-0.10	1.54	0.65	1.21	1.81
$b_{22}$	1.29	0.40	0.11	1.42	0.09
$b_{12}$	-0.90***	0.00	-0.10	-0.54**	-0.04
$b_{21}$	0.46*	-0.24	-0.31***	0.33*	0.65
$b_{10}$	0.36	0.75	0.21	0.32	0.89
$b_{20}$	-0.03	0.33	-0.08	-0.03	0.06
$a$	0.55	0.21	0.44	0.48	0.46
$\sigma_1$	0.39	0.00	0.38	0.00	0.00
$\sigma_2$	0.00	0.53	0.60	0.00	0.65
$\nu_1$	0.00	-0.40	0.29	0.35	-0.17
$\nu_2$	0.49	0.00	0.08	0.52	0.00
LL	-70.87	-79.76	-72.81	-73.68	-59.56
LRT $\chi^2_2$	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

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645 Fig. 1: Detrended sediment core data for midge egg capsules and diatoxanthin, echinenone,  
646 alloxanthin,  $\beta$ -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.

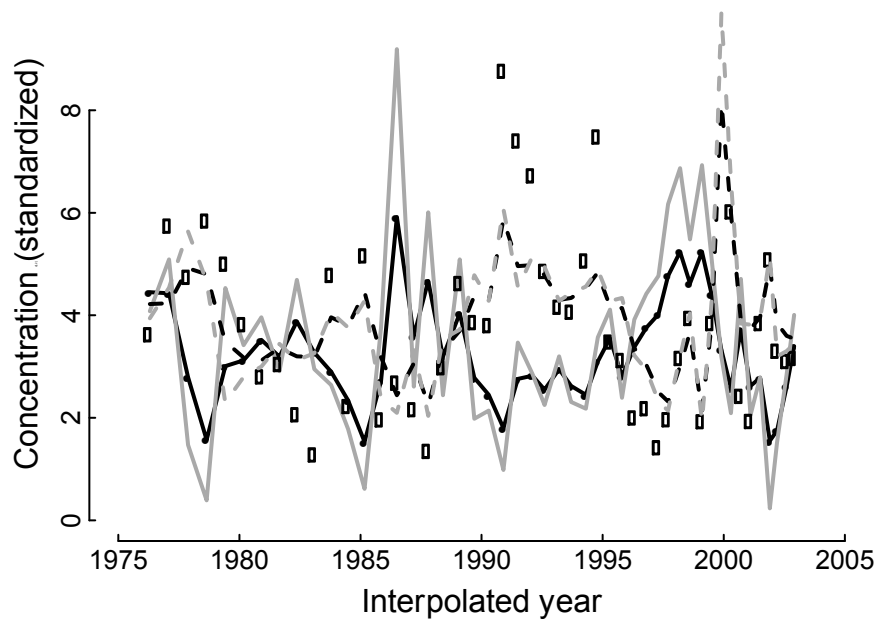
650  
651 Fig. 2: Fit of the state-space model (Eqs. 2, 3) to detrended diatoxanthin (solid dots) and midge  
652 egg capsule abundance (open dots). Solid and dashed black lines give the fit of the model to the  
653 observed values  $x^*(t)$  and  $u^*(t)$  of diatoxanthin and midges (Eq. 3), whereas the solid and dashed  
654 gray lines give the estimates of the deposition rates prior to sediment mixing (Eq. 2).



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