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ARTICLE

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Reconstructing midge consumer–resource dynamics using carbon stable isotope signatures of archived specimens

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Abstract

Population cycles can be caused by consumer–resource interactions. Confirming the role of consumer–resource interactions, however, can be challenging due to an absence of data for the resource candidate. For example, interactions between midge larvae and benthic algae likely govern the high-amplitude population fluctuations of *Tanytarsus gracilentus* in Lake Mývatn, Iceland, but there are no records of benthic resources concurrent with adult midge population counts. Here, we investigate consumer population dynamics using the carbon stable isotope signatures of archived *T. gracilentus* specimens collected from 1977 to 2015, under the assumption that midge $\delta^{13}C$ values reflect those of resources they consumed as larvae. We used the time series for population abundance and $\delta^{13}C$ to estimate interactions between midges and resources while accounting for measurement error and possible preservation effects on isotope values. Results were consistent with consumer–resource interactions: high $\delta^{13}C$ values preceded peaks in the midge population, and $\delta^{13}C$ values tended to decline after midges reached high abundance. One interpretation of this dynamic coupling is that midge isotope signatures reflect temporal variation in benthic algal $\delta^{13}C$ values, which we expected to mirror primary production. Following from this explanation, high benthic production (enriched $\delta^{13}C$ values) would contribute to increased midge abundance, and high midge abundance would result in declining benthic production (depleted $\delta^{13}C$ values). An additional and related explanation is that midges deplete benthic algal abundance once they reach peak densities, causing midges to increase their relative reliance on other resources including detritus and associated microorganisms. Such a shift in resource use would be consistent with the subsequent decline in midge $\delta^{13}C$ values. Our study adds evidence that midge–resource interactions drive *T. gracilentus* fluctuations and demonstrates a novel application of stable isotope time-series data to understand consumer population dynamics.

KEYWORDS

benthic primary production, Chironomidae, detritus, diatoms, Mývatn, population fluctuation, time series

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INTRODUCTION

Cyclic population dynamics are widespread and can be caused by a variety of factors, including trophic interactions. For primary consumers, interactions with either their exploiters (e.g., predators, pathogens) or their resources (e.g., primary producers) may underly cyclic dynamics (Krebs, 2011; Turchin et al., 2003). The dynamic outcomes of such interactions may vary depending on the properties of both the consumer and the resource. For example, aquatic primary producers are generally small relative to primary consumers and more edible than terrestrial plants (Shurin et al., 2006; Strong, 1992). Herbivory is also greater in aquatic ecosystems, with primary consumers removing a higher proportion of net primary production compared with terrestrial ecosystems (Cyr & Pace, 1993). Although severe biomass reduction is not essential for primary producers to regulate herbivore populations (Abbott & Dwyer, 2007), the often-high consumption of primary producers suggests that top-down control by primary consumers is prevalent in aquatic systems (Shurin & Seabloom, 2005). Thus, aquatic primary consumer populations may be particularly affected by resource limitation (Lancaster & Downes, 2018).

Disentangling consumer–resource interactions often requires data covering multiple population cycles for both the consumer and the resource. However, data for one ecological partner are commonly lacking, which complicates identifying consumer–resource interactions as a cause of population fluctuations (Bjørnstad & Grenfell, 2001; Einarsson et al., 2016). Measuring primary producer biomass and/or productivity often involves methods distinct from those used to monitor consumer populations. Thus, direct resource availability data may not accompany many long-term records of primary consumer abundance. While it is possible to infer the general causes underlying cyclic dynamics by analyzing a single consumer population (Kendall et al., 1999), surrogate data for otherwise absent information about resource abundance may help to identify the role of consumer–resource interactions in generating population cycles.

Here, we examine a primary consumer population with widely fluctuating abundance and characterize the extent to which consumer–resource interactions are linked to these fluctuations. *Tanytarsus gracilentus* (Diptera: Chironomidae) is a keystone species in Lake Mývatn (Icelandic for "midge lake") that undergoes large fluctuations in population size, spanning five to six orders of magnitude, with irregularly timed crashes occurring every 4–10 years. Larvae feed on benthic diatoms and detritus from silken tubes that they construct within surface sediment (Ingvason et al., 2004). Our working hypothesis is that consumer–resource interactions drive *T. gracilentus* fluctuations. Support for this hypothesis includes cyclic dynamics between diatom pigments (diatoxanthin) and midge abundance (egg capsules) that were found in sediment cores from Mývatn (Einarsson et al., 2016). Decades of monitoring adult midges (1977 to the present) capture detailed and extensive information on *T. gracilentus* population abundance. However, concurrent data for resource candidates do not exist, so we have no direct way to use these long-term adult data to analyze fluctuations in midge abundance together with their resources. Nonetheless, using resource surrogates gives indirect evidence for consumer–resource interactions. Wing lengths (a surrogate for food abundance and/or quality) decline in generations preceding a crash, while there is no relationship between *T. gracilentus* and predator abundance (Einarsson et al., 2002). Additionally, a consumer–resource model allowing for alternative dynamical states between a relatively stable high point and a high-amplitude cycle closely matches the observed *T. gracilentus* abundance data (Ives et al., 2008). A final argument for the importance of consumer–resource interactions is the lack of evidence that other factors (e.g., diseases, climatic variability) cause *T. gracilentus* population crashes, although absence of evidence is not necessarily evidence of absence.

In the absence of direct data on midge resources, we used carbon stable isotope time-series data to assess the importance of consumer–resource interactions to *T. gracilentus* population fluctuations. Specifically, we treated the δ^{13}C signatures of archived specimens collected during the long-term midge monitoring at Mývatn as a surrogate for the resources consumed during their larval stage, and we used a multivariate autoregressive model to quantify interactions between *T. gracilentus* abundance and δ^{13}C values. The isotopic composition of resources assimilated by consumers can be inferred from the consumer's δ^{13}C signatures because little carbon isotopic fractionation occurs between consumers and their diets (Peterson & Fry, 1987). By analyzing the joint time series for *T. gracilentus* population abundance and δ^{13}C values, we assessed whether their dynamics showed the signatures of consumer–resource interactions. Moreover, this application of stable isotope data may add information regarding the mechanisms underlying consumer–resource interactions that are difficult to infer from previously used resource surrogates (e.g., wing lengths; Einarsson et al., 2002). Temporal variation in consumer δ^{13}C signatures may reflect a shift in the isotopic baseline of their predominant resource (Grey et al., 2009; Olden et al., 2019) or dietary changes (Blight et al., 2015; Hanson et al., 2017). For example, the δ^{13}C values of benthic algae are positively correlated with primary productivity rates (Devlin et al., 2013) and biomass (Hill et al., 2008; Hill & Middleton, 2006), and epipelic diatoms are a prevalent dietary component of *T. gracilentus*. Thus, we hypothesize that the $\delta^{13}C$ time series may represent a proxy for the availability of benthic diatoms to *T. gracilentus* across its population fluctuations. A second, nonmutually exclusive hypothesis is that $\delta^{13}C$ variation indicates shifts in resource reliance (e.g., diatoms versus detritus; benthic-derived versus pelagic-derived carbon) across *T. gracilentus* population fluctuations.

METHODS

Study system, chironomid monitoring, and isotope sampling

Mývatn is a large (37 km^2), shallow (2.5 m mean depth) lake in northeast Iceland (65°40′ N; 17°00′ W). It is naturally eutrophic and supports high primary production (Phillips, 2020), while receiving little allochthonous inputs (Jónasson, 1979). Benthic algae generally dominate whole-lake primary production (McCormick et al., 2021), in particular, diatoms (especially Fragilariaceae) are the dominant primary producers on the sediment substrate (Einarsson et al., 2004). Macrophytes are largely restricted to the eastern portion of the lake near the spring water inputs and are uncommon throughout the Mývatn's profundal habitat (Einarsson et al., 2004). Phytoplankton production, in the large part due to cyanobacteria blooms, varies interannually (Einarsson et al., 2004; McCormick et al., 2021). Episodic cyanobacteria blooms can contribute substantially to total production (McCormick et al., 2021; Phillips, 2020), although they fail to develop in some summers.

T. gracilentus larvae make up the majority of Mývatn's secondary production in years of high abundance, with densities of >200,000 individuals m^{-2}, and they are nearly absent in crash years (Lindegaard & Jónasson, 1979). As larvae, *T. gracilentus* construct silken tubes at the sediment surface from which they feed. *T. gracilentus* larvae primarily consume diatoms and detritus, and gut content analyses suggest moderate variation in resource selectivity across instars, with first instars consuming a higher proportion of diatoms and fourth instars consuming relatively more detritus (Ingvason et al., 2004). Recent research indicates that the $\delta^{13}C$ signatures of late instar *T. gracilentus* larvae differ from those of surface sediment, implying that larvae feed selectively upon ^{13}C-enriched resources (McCormick, Phillips, Botsch, Ólafsson, et al., 2022), which are likely to include the most productive diatom layer (sensu Devlin et al., 2013). It is worth noting that previous studies provide only static accounts of *T. gracilentus* feeding, as they do not examine possible changes in resource use across population cycles.

Nonoverlapping spring and summer *T. gracilentus* generations generally occur each year, with adults emerging in early June and early August. For individuals that emerge in summer, rapid larval growth occurs in a 2-month period over June and July. Individuals comprising the spring emergence typically overwinter in diapause in the third instar and transition to fourth instar the following April (Ingvason et al., 2004; Lindegaard & Jónasson, 1979). Adult *T. gracilentus* are short-lived and are generally thought not to feed, although feeding (e.g., on nectar and pollen) has been observed for some other chironomid species (Armitage, 1995).

Since 1977, chironomid abundances at Mývatn have been monitored with lakeshore window traps. Window traps passively capture aerial insects and consist of an open box containing a preservative situated 1–3 m above the water surface (see Jonsson et al., 1986 and Gardarsson et al., 2004 for details). For this study, the focal window trap was located on the Syðri-Neslönd peninsula and captures a chironomid assemblage characteristic of the profundal habitat (Gardarsson et al., 2004). Window traps were sampled from May to September every 1–2 weeks. All dipteran taxa were enumerated and identified to species (typically with subsampling). *T. gracilentus* abundances were summed within spring and summer periods (using a cutoff date of 15–20 July), which distinguishes the two annual emergences (Gardarsson et al., 2004). After sample processing, archived specimens were preserved in 70% ethanol for long-term storage.

We retrieved *T. gracilentus* adults collected from 1977 to 2015 for $\delta^{13}C$ analysis. Our target was 60 adults per sample, and we otherwise collected as many individuals as possible. During some population crashes, we could not obtain enough material for isotopic analysis (Appendix S1: Figure S1). We generally retrieved specimens from one sample date per emergence, although we examined variability among dates by collecting specimens from two dates for a subset of emergences (Appendix S1). Variation in *T. gracilentus* $\delta^{13}C$ values for specimens from different dates within the same emergence was similar to the variation for different specimens from within same window trap (sample date) (Appendix S1: Figure S2).

Adult midges were exposed to chemical preservatives in the window trap and then transferred to long-term storage in ethanol. The original window trap preservative was formalin, but this was changed to ethylene glycol in 1996 and later to propylene glycol in either 2008 or 2009. We accounted for the different preservatives in our statistical model (see *Methods: Time-series analysis*). Also, in a small experiment, we examined how two of the preservatives (formalin and propylene glycol followed by ethanol storage) affected $\delta^{13}C$ values (Appendix S2); however, we did not examine ethylene glycol effects.

Specimens for isotopic analysis were rinsed with deionized water, dried at 60°C, homogenized with a pestle, stored in a desiccator for 24 h, and then weighed into tin capsules. The University of California Davis Stable Isotope Laboratory (Davis, CA, USA) performed the isotopic analysis. Isotope signatures are expressed in delta notation where $\delta = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$. δ^{13}C is reported relative to Vienna PeeDee Belemnite. Analytical error standard deviation was <0.10‰ (Appendix S1). Duplicates run for a subset of homogenized samples had a mean standard deviation of 0.07‰ (Appendix S1: Figure S2).

Because benthic diatoms are an important dietary component for *T. gracilentus*, we hypothesized that shifts in baseline algal δ^{13}C signatures could contribute to variation in midge isotope values. Previous studies have documented the effects of primary production and benthic algal abundance on δ^{13}C values (Devlin et al., 2013; Hill et al., 2008; Hill & Middleton, 2006). To verify this potential interpretation, we examined the relationship between benthic primary production and δ^{13}C values in a supplemental field experiment conducted in Mývatn (Appendix S3). Supplemental results support a significant positive association between δ^{13}C values and benthic primary production, although the magnitude of this effect (i.e., in terms of the range in sediment δ^{13}C values across the light treatments) was low compared with the observed variation in the midge δ^{13}C time series (Appendix S3).

Time-series analysis

We used a multivariate autoregressive state-space model to examine the interactions between midge abundance and δ^{13}C values (Harvey, 1989; Ives et al., 2003). When multiple samples within an emergence were analyzed, we used the mean δ^{13}C value. Prior to analysis, we log-transformed *T. gracilentus* abundance and then *z*-transformed the log-abundance and δ^{13}C values by subtracting the mean and dividing by the standard deviation.

Consumer–resource dynamics were modeled as:

$$x_1(t) = b_{10} + b_{11}[x_1(t-1) - b_{10}] + b_{12}[x_2(t-1) - b_{20}] + \varepsilon_1(t)$$

$$x_2(t) = b_{20} + b_{22}[x_2(t-1) - b_{20}] + b_{21}[x_1(t-1) - b_{10}] + c_{21}U_1(t) + \varepsilon_2(t)$$

where $x_1(t)$ and $x_2(t)$ are the transformed *T. gracilentus* abundance and δ^{13}C value in generation *t*; coefficients b_{ij} quantify the effect of $x_j(t-1)$ on $x_i(t)$, such that b_{12} represents the effect of δ^{13}C on the change in midge abundance, and b_{21} represents the effect of midge abundance on the change in δ^{13}C; b_{ii} represents the autocorrelation of $x_i(t)$ between generations; b_{i0} scales mean values for each state variable; and $\varepsilon_i(t)$ is a normal random variable with mean zero and variance σ_i^2 representing variability for each state variable. The time variable *t* represents the generation (spring and summer), which is the natural time-step to study *T. gracilentus* consumer–resource interactions. Visual inspection of δ^{13}C values suggested that spring generation midges were ^{13}C-depleted relative to those from the summer generation of the same year. Therefore, we included a covariate, $U_1(t)$, to account for season (value zero for spring and one for summer), with c_{21} giving the effect of season on $x_2(t)$.

We incorporated measurement error for $x_1(t)$ and $x_2(t)$ in the observation equations:

$$x_1(t)^* = x_1(t) + \varphi_1(t)$$

$$x_2(t)^* = x_2(t) + c_{22}U_2(t) + c_{23}U_3(t) + \varphi_2(t)$$

where $x_1(t)^*$ and $x_2(t)^*$ are the observed transformed *T. gracilentus* abundance and δ^{13}C values; $\varphi_1(t)$ is a Gaussian random variable with mean zero and variance υ_1^2 representing observation error for *T. gracilentus* log-abundance. To account for differences in sample sizes in the isotope analyses, $\varphi_2(t)$ is a Gaussian random variable with mean zero and variance $\upsilon_2^2/n(t)$, where $n(t)$ is the number of individuals pooled for isotopic analysis. We coded the window trap preservative with two categorical covariates: $U_2(t)$ for ethylene glycol, which had value one for 1996–2007 and zero otherwise, and $U_3(t)$ for propylene glycol, which had value one for 2008–2015 and zero otherwise. This allows the mean δ^{13}C to differ by preservative methodology, such that c_{22} and c_{23} respectively represent the deviation of δ^{13}C values due to ethylene glycol or propylene glycol preservation in the window trap compared with formalin. It is uncertain whether the transition from ethylene glycol to propylene glycol occurred in 2008 or 2009, but assuming 2009 rather than 2008 did not change the conclusions from the analyses (Appendix S4).

We fitted the state-space model with a Kalman filter using code modified from Ives and Dakos (2012) using R version 4.0.3 (R Core Team, 2020). Fitting the model resulted in maximum likelihood estimates for 13 parameters: b_{10}, b_{20}, b_{11}, b_{22}, b_{12}, b_{21}, c_{21}, c_{22}, c_{23}, σ_1^2, σ_2^2, υ_1^2, and υ_2^2. To determine the statistical significance of the effect of δ^{13}C on midge abundance (i.e., $b_{12} \neq 0$) and the effect of midge abundance on δ^{13}C ($b_{21} \neq 0$), we compared the full model with a reduced 11-parameter model (where

$b_{12} = b_{21} = 0$) using a likelihood ratio test. We also tested the significance of b_{12} and b_{21} separately by comparing the full model to a reduced 12-parameter model where either $b_{12} = 0$ or $b_{21} = 0$. This allowed us to isolate consumer effects on the resource, as well as resource effects on the consumer. Values for δ^{13}C were missing for 13 of 78 generations; in the state-space model, these generations were included in the process equations but were skipped over in the observation equations.

RESULTS

Results from the time-series analysis were consistent with dynamics that would arise from consumer–resource interactions in which δ^{13}C values are a surrogate for midge resources. High δ^{13}C values tended to precede peak *T. gracilentus* abundances, and δ^{13}C values tended to decline when midges reached high abundance (Figure 1). These patterns were quantified by the state-space model: the effect of δ^{13}C on *T. gracilentus* abundance in the subsequent generation (b_{12}) was positive, while the reciprocal effect (b_{21}) was negative (Table 1). Also, b_{12} and b_{21} were significantly different from zero when analyzed together ($b_{12} = b_{21} = 0$: $\chi^2(2) = 13.37$; $p = 0.0012$) and separately ($b_{12} = 0$: $\chi^2(1) = 5.99$, $p = 0.0144$; $b_{21} = 0$: $\chi^2(1) = 8.90$, $p = 0.0029$). These results suggested that *T. gracilentus* population abundance and δ^{13}C values are dynamically coupled.

The model also demonstrated a seasonal effect on *T. gracilentus* δ^{13}C values, represented by the positive estimate for c_{21} (Table 1; Figure 1): midges from the summer generation generally had higher δ^{13}C values relative to those from the spring generation of the same year (mean difference ± SD = 1.17‰ ± 1.45‰). Midge abundance and δ^{13}C values showed moderately high temporal autocorrelation as indicated by b_{11} and b_{22}.

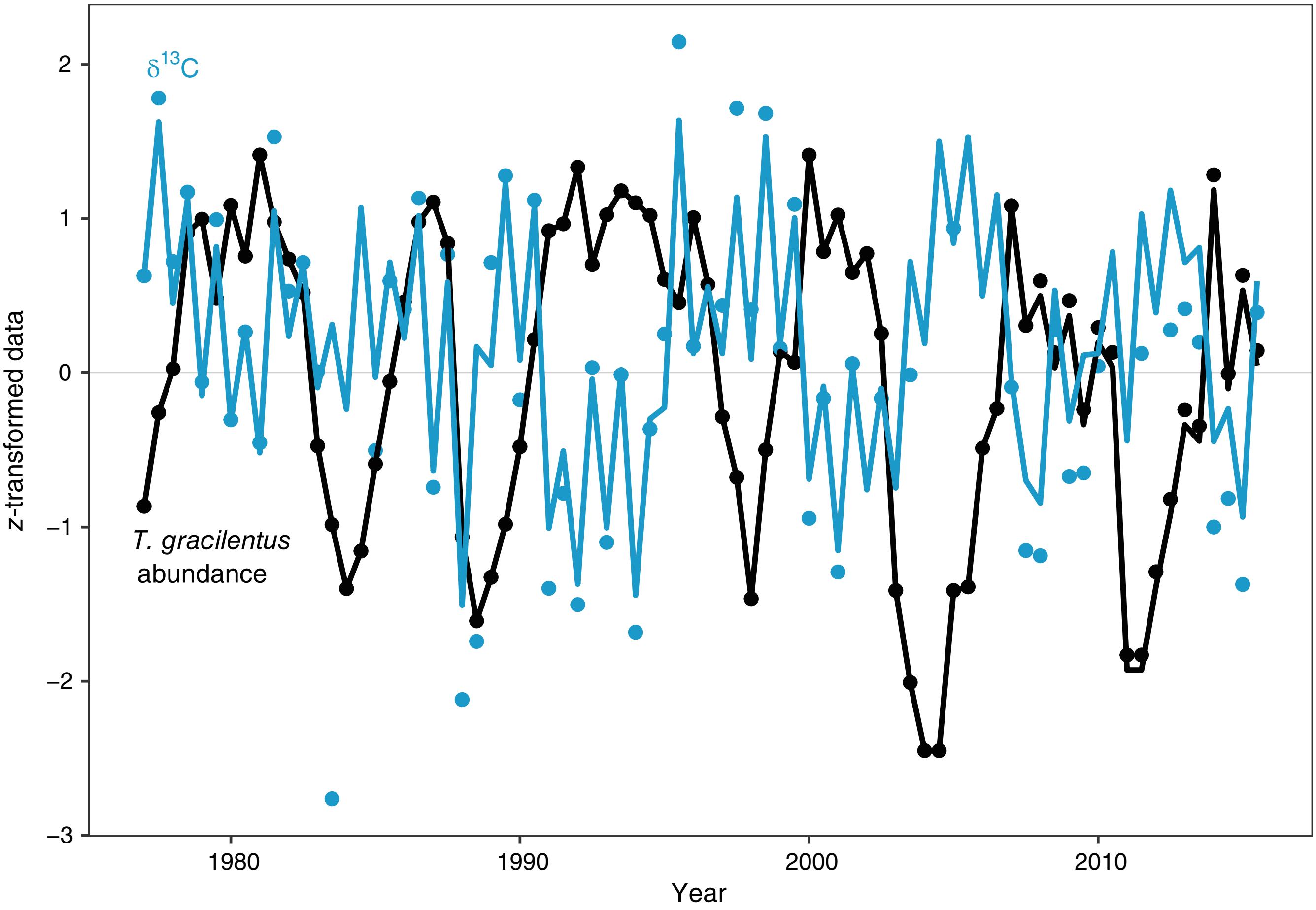

FIGURE 1 Solid lines show model fits to *T. gracilentus* abundance (black) and δ^{13}C values (blue). Points show *z*-transformed data. The model fits give one-step-ahead predictions from the Kalman filter; because the estimate of the observation error for *T. gracilentus* abundance was zero (Table 1), these predictions fitted the points closely. This does not mean, however, that the model fitted the data perfectly, because there is still process error that is not depicted in the one-step-ahead predictions.

TABLE 1 Parameter estimates from the state-space model.

Coefficient	Estimate	Description
b_{10}	−1.07	Mean scaled value for *T. gracilentus* abundance
b_{20}	−0.57	Mean scaled value for $\delta^{13}C$ values
b_{11}	0.83	Autocorrelation of *T. gracilentus* abundance
b_{22}	0.45	Autocorrelation of $\delta^{13}C$ values
b_{12}	0.25	Effect of $\delta^{13}C$ values on the change in *T. gracilentus* abundance
b_{21}	−0.27	Effect of *T. gracilentus* abundance on the change in $\delta^{13}C$ values
c_{21}	1.39	Seasonal effect (summer relative to spring) on $\delta^{13}C$ values
c_{22}	0.10	Ethylene glycol effect (relative to formalin) on $\delta^{13}C$ values
c_{23}	−0.38	Propylene glycol effect (relative to formalin) on $\delta^{13}C$ values
σ_1	0.61	Process error (SD) for *T. gracilentus* abundance
σ_2	0.52	Process error (SD) for $\delta^{13}C$ values
υ_1	0.00	Observation error (SD) for *T. gracilentus* abundance
υ_2	2.83	Observation error (SD) for $\delta^{13}C$ values

The low magnitude for coefficient c_{22} suggests that ethylene glycol as the window trap preservative had little effect on mean $\delta^{13}C$ values. The negative estimate for c_{23} suggests that propylene glycol resulted in lower mean $\delta^{13}C$ values compared with formalin (Table 1); however, this is inconsistent with our experimental results comparing storage effects of propylene glycol/ethanol and formalin/ethanol (Appendix S2). The reason for this discrepancy between the model and supplemental experiment results is uncertain, but potential contributing factors include differences in study organism (black flies in the experiment vs. midges in the time series) or isotopic signatures of chemical preservatives (long-term monitoring vs. our experiment) (Appendix S2). While we performed the supplemental experiment to understand how chemical preservation may affect archived specimens, our statistical approach provided us with an alternate way to account for this potential artifact, and model results were similar regardless of whether or not c_{22} and/or c_{23} were included in the model. Finally, the lack of correspondence between our model coefficient estimate and supplemental experiment should not encumber interpretation of temporal $\delta^{13}C$ patterns because chemical preservation effects were not affected by storage duration (Appendix S2).

DISCUSSION

Our study examined the fluctuations of *T. gracilentus* abundances across a multidecade time series and used $\delta^{13}C$ isotope values to infer consumer–resource interactions. While an extensive record of the adult *T. gracilentus* population dynamics exists, there are no direct, concurrent data for resource availability. We treated $\delta^{13}C$ values of archived specimens collected from a monitoring program as a resource surrogate and found that population abundance and $\delta^{13}C$ values were dynamically coupled, providing support that the interaction between *T. gracilentus* and their resources underlies the population fluctuations in Mývatn. We present several possible mechanisms related to *T. gracilentus* resource use that could contribute to the cycling between their carbon isotope values and population abundance.

In studies analyzing stable isotopes of bulk tissues, detecting mechanisms responsible for temporal variation in consumer signatures is often challenging because multiple factors may contribute to the variation. For example, both altered isotopic baselines (e.g., due to conditions affecting primary producers) and changes in feeding behavior (e.g., due to dietary shifts) can affect consumer isotope values (Blight et al., 2015; Grey et al., 2009; Hanson et al., 2017; Olden et al., 2019; Wainright et al., 1993). Nonetheless, ecological context regarding study systems and organisms (e.g., trophic level, feeding habits) assists in interpreting probable mechanisms underlying temporal variation in consumer isotope signatures (Grey et al., 2009; Olden et al., 2019). In our system, allochthonous inputs are low, and *T. gracilentus* is a known herbivore/detritivore. Thus, we suggest that the variation in midge $\delta^{13}C$ values across their population fluctuations is likely to be due to one or a combination of the following explanations: (i) changes in the productivity and/or biomass of benthic diatoms, (ii) shifts in midge consumption between diatoms and detritus, or (iii) shifts in midge consumption between benthic and pelagic carbon.

Changes in the productivity and/or biomass of benthic diatoms

The well documented relationship between metrics of algal growth and carbon isotope signatures supports the interpretation that *T. gracilentus* $\delta^{13}C$ values reflect the dynamics of benthic algae. Carbon isotope signatures of aquatic primary producers are influenced by the $\delta^{13}C$ of available dissolved inorganic carbon (DIC) and the extent of fractionation during carbon uptake (Finlay, 2004; Keeley & Sandquist, 1992), which occurs because ^{12}C

reacts more quickly than ^{13}C in biochemical reactions (Peterson & Fry, 1987). In particular, benthic algae have a limited carbon supply due to thick boundary layers (stagnant water separating periphyton from the overlying water) that slow DIC diffusion; consequently, benthic algae discriminate less against ^{13}C and may use bicarbonate if CO_2 becomes limiting, leading to their relatively high δ^{13}C values (Hecky & Hesslein, 1995; Hill & Middleton, 2006). The association between algal δ^{13}C values and primary production is due to the relationship between photosynthetic rates and DIC demand. High rates of primary production exacerbate carbon limitation, and increased DIC demand relative to availability reduces photosynthetic fractionation, so that rates of high primary production are associated with high δ^{13}C values (Devlin et al., 2013; Hecky & Hesslein, 1995). Empirically, δ^{13}C signatures are also positively related to benthic algal biomass because inorganic carbon becomes depleted in thicker algal assemblages due to high photosynthetic activity and diffusion-limited movement of DIC into the periphyton matrix (Hill et al., 2008; Hill & Middleton, 2006). For consumers that predominantly rely on benthic algal carbon, the above-described relationships suggest that aquatic primary consumer δ^{13}C values should reflect primary production (Devlin et al., 2013), providing a potential surrogate for resource availability.

Previous work has documented the interaction between benthic primary production and *T. gracilentus* dynamics. For example, low-to-moderate experimental densities of *T. gracilentus* larvae enhance benthic primary production by increasing substrate availability through their tube building (Phillips et al., 2019). However, the relationship between larval density and primary production is nonlinear and, at high larval densities, consumption of benthic algae may outweigh their substrate-boosting effect (Phillips et al., 2021). Thus, it is likely that high *T. gracilentus* densities negatively affect primary production (Phillips et al., 2021), which is consistent with our results if δ^{13}C is treated as a surrogate for benthic algal production. Moreover, in a paleoecology study at Mývatn, high concentrations of diatom pigments were associated with increased midge egg capsule abundance, and increased midge abundance was associated with declines in the diatom pigment (Einarsson et al., 2016), suggesting that midges reduce diatom biomass as their population grows. Decreased diatom abundance could reduce competition among algae for inorganic carbon, and thereby enable higher ^{13}C-discrimination (i.e., more depleted δ^{13}C values). Finally, our experiment manipulating light levels showed a positive association between δ^{13}C values and benthic primary production, although this relationship entailed a lower range of δ^{13}C values than that observed in our midge isotope time series (Appendix S3). Overall, the interpretation that δ^{13}C values reflect benthic algae consumed by larvae is consistent with other lines of evidence supporting that midge–diatom interactions drive the *T. gracilentus* population fluctuations in Mývatn.

Shifts in midge consumption between diatoms and detritus

A second explanation underlying the coupling between *T. gracilentus* population abundance and δ^{13}C values involves a shift in their relative reliance on diatoms and detritus. Considering that benthic algae comprise a large proportion of whole-lake production in Mývatn, a majority of the detrital pool within the sediment is likely to be from benthic-derived carbon. While selectivity for diatoms and detritus has been documented across larval instars within a generation and between two subsequent generations (Ingvason et al., 2004), *T. gracilentus* use of these two resources has not been empirically examined across its high-amplitude population cycles. Like explanation (i), the positive estimate for b_{12} may indicate an association between high primary productivity and increases in midge population abundance, especially if diatoms represent a high-quality resource (Fuller & Mackay, 1981; Rosillon, 1988). If *T. gracilentus* overexploit benthic diatoms once they reach peak population abundances, then larvae may consequently rely more heavily on detritus from within the sediment. In support of this, a consumer–resource model suggests that detritus may provide an alternate food source to larvae when diatoms become depleted due to the consumption by midges at high population densities (Ives et al., 2008). Additionally, estimates of *T. gracilentus* secondary production can exceed benthic primary production for short periods of time (J. Botsch, unpublished data), suggesting that the larval population can indeed require more energy than that supported by the current primary production. Secondary production of primary consumers has shown to be coupled with primary production in other high-latitude systems, whereby benthic macroinvertebrates show seasonal shifts in their reliance on diatoms and organic matter (Huryn & Benstead, 2019). The negative estimate for b_{21}, with decreased δ^{13}C values following high midge abundance, would be consistent with a shift toward detritivory. For example, low chironomid carbon isotope signatures may be associated with consumption of ^{13}C-depleted resources, such as detritus and associated microorganisms (Fiskal et al., 2021; McCormick, Phillips, Botsch, Ólafsson, et al., 2022; McGoldrick et al., 2008). In summary, periods where *T. gracilentus* feed more heavily on productive diatoms may be associated with increases in their population abundance, while higher relative reliance on detrital pathways may coincide with population declines.

Shifts in midge consumption between benthic and pelagic carbon

A third explanation for the variation in *T. gracilentus* $\delta^{13}C$ values is a dietary shift toward reliance on phytoplankton. Pelagic primary production is generally low in Mývatn except during intermittent cyanobacteria blooms and, compared with benthic algae, pelagic primary producers tend to have lower $\delta^{13}C$ values (Hecky & Hesslein, 1995). In a small number of concurrently collected benthic and pelagic samples from Mývatn, benthic sediment was ^{13}C-enriched compared with isotope samples from the pelagic habitat, although the differences in isotopic signatures were quite small (McCormick, Phillips, Botsch, Ólafsson, et al., 2022). Under alternate hypothesis (iii), our statistical results (the negative b_{21} estimate) would imply that high *T. gracilentus* population abundance increases their reliance on pelagic primary production (lower $\delta^{13}C$ values). However, high *T. gracilentus* densities stabilize surface sediments and thereby are expected to inhibit phosphorus release from the sediment to the water column, which should in principle limit cyanobacteria blooms (Einarsson et al., 2004). Thus, the interpretation corresponding to explanation (iii) is inconsistent with our current knowledge of Mývatn's ecology. Although, we acknowledge that the described inconsistencies between our ecological understanding and the hypothetical coupling between *T. gracilentus* abundance and shifting reliance on pelagic-derived carbon are largely based on inference rather than direct evidence, and a lack of temporal data comparing benthic and pelagic resources complicates assessing the importance of this potential mechanism. Even so, previous studies have found a lack of evidence linking midge population fluctuations and phytoplankton. For example, in previously analyzed sediment cores, no association between midge abundance and cyanobacteria pigments was detected (Einarsson et al., 2016). Thus, we suggest a shifting reliance between pelagic and benthic-derived carbon is a less likely mechanism for the observed midge $\delta^{13}C$ patterns compared with the explanations (i) and (ii) that link these dynamics to interactions with benthic resources.

Our results revealed seasonal effects on $\delta^{13}C$ values, as *T. gracilentus* $\delta^{13}C$ values were typically higher in summer than spring generations for a given year. These isotopic differences could reflect seasonal patterns of benthic primary productivity. Despite the late ice-off at Mývatn (generally mid May), benthic photosynthesis is likely to occur under the ice in spring (Ólafsson, 1979) because light can penetrate ice once the snow has melted (Karlsson et al., 2008). However, summer provides much greater light availability than spring, which could contribute to higher benthic productivity and the associated higher midge $\delta^{13}C$ values. Differences in $\delta^{13}C$ signatures of DIC used by algae for carbon fixation could further affect the seasonal pattern in midge $\delta^{13}C$ values. We lack $\delta^{13}C$ data for the DIC pool over our time series, but bicarbonate may comprise much of Mývatn's DIC pool during the summer, as pH is generally >9 (Boyd, 2000; Ólafsson, 1979; Thorbergsdóttir & Gíslason, 2004). In winter pH can decline to 7–8 (Ólafsson, 1979; Thorbergsdóttir & Gíslason, 2004), which may elevate the aqueous CO_2 fraction of the DIC pool. A compositional change in available DIC could influence algal isotope signatures because bicarbonate is ^{13}C-enriched compared with aqueous CO_2 (Hecky & Hesslein, 1995). Ice cover also affects DIC composition by preventing atmospheric CO_2 influx. Thus, a prevalent source of carbon for photosynthesis under ice is likely to have come from heterotrophic respiration of benthic detritus (Karlsson et al., 2008), which could influence algal $\delta^{13}C$ values, as CO_2 derived from microbial degradation of organic matter is ^{13}C-depleted compared with atmospheric CO_2 (Hecky & Hesslein, 1995). Overwintering larvae may also alter their feeding habits, possibly resulting in the assimilation of ^{13}C-depleted resources. Nonetheless, explanations for seasonal changes in $\delta^{13}C$ do not contradict the overall, long-term patterns consistent with consumer–resource interactions.

Statistical autocorrelation measures how quickly variables change through time, and autocorrelation of *T. gracilentus* abundance (b_{11}) and $\delta^{13}C$ values (b_{22}) revealed additional biologically relevant information. If $\delta^{13}C$ values were to largely reflect benthic algae (i.e., explanation (i)), lower autocorrelation in $\delta^{13}C$ compared with midge abundance may be expected because turnover times of diatoms are much shorter than generation times of midges. While lower than for midges, $\delta^{13}C$ still had substantial autocorrelation, which may suggest that factors that operate on slower time scales relative to turnover times of algal cells may have affected midge isotopic signatures. Possibilities include the positive substrate-boosting effect of midges (through their tube building) on algal productivity, which changes on a similar time scale as midge generations, and the supply of nutrient reserves in the sediment that limits algal productivity, which may also operate on a delayed time scale if they are affected by midges (e.g., if midges affect nutrient cycling by excreting nutrients into the pelagic zone, leading to nutrient depletion in the sediment in subsequent generations). Similar magnitudes in the autocorrelation for midge population and isotope signatures would also be compatible with the alternative explanation that δ^{13}C values largely reflect a shifting reliance on diatoms and detritus (i.e., explanation (ii)), whereby the change in relative resource use is driven by overexploitation by larvae at high population densities. While consumer δ^{13}C signatures are influenced by the isotopic turnover rates of their tissues, we assume that δ^{13}C values of archived adults reflect those of late instar larvae and that larval isotopic turnover rates would be similar across the time series of midge generations; thus, we do not expect larval tissue turnover to directly impact the autocorrelation of midge δ^{13}C signatures from one generation to the next.

We propose that interactions between midge larvae and benthic resources are the most compelling explanations for the coupled dynamics between *T. gracilentus* population abundance and δ^{13}C values. Specifically, these interactions may involve variation in the isotopic signatures of benthic algae and/or shifts in larval reliance on benthic diatoms versus detritus. Both mechanisms suggest the integral nature of benthic algae to midge fluctuations, such that our study provides additional evidence that *T. gracilentus* dynamics are an example in which interactions between primary consumers and primary producers can cause large fluctuations in abundance.

Archived specimens provide opportunities to understand ecological processes, with previous studies analyzing temporal trends of consumer stable isotope signatures to retrospectively examine changes in resource use, food web structure, and ecosystem function (Blight et al., 2015; Grey et al., 2009; Hanson et al., 2017; Vander Zanden et al., 2003; Wainright et al., 1993). While previous studies have considered stable isotope data as an explanatory factor for population trends (Blight et al., 2015; Wainright et al., 1993), to our knowledge the explicit application of isotope signatures to examine consumer–resource dynamics is novel to our study. If paired with time-series data on population abundance, isotopic analysis of archived specimens may similarly lead to insights regarding the dynamics of other consumer populations from other systems. We suggest that our approach may be particularly useful for investigating consumer–resource interactions when long-term resource data are otherwise lacking and for consumers with relatively known feeding habits.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (McCormick, Phillips, Botsch, Einarsson, et al., 2022) are available on Figshare at https://doi.org/10.6084/m9.figshare.c.6197266.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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