OIKOS

Research article

Aquatic insects balance growth with future supply of algal food resources

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Oikos
2023: e09902
doi: 10.1111/oik.09902
Subject Editor: Steven Declerck
Editor-in-Chief: Dries Bonte
Accepted 20 July 2023

Many consumers depend on the contemporaneous growth of their food resources. For example, *Tanytarsus gracilentus* midges feed on algae, and because midge generation time is much longer than that of algae, individual midges benefit not just from the standing stock but also from the growth of algae during their lifespans. This implies that an intermediate consumption rate maximizes midge somatic growth: low consumption rates constrain midge growth because they do not fully utilize the available food, whereas high consumption rates suppress algal biomass growth and consequently limit future food availability. An experiment manipulating midge presence and initial algal abundance showed that midges can suppress algal growth, as measured by changes in algal gross primary production (GPP). We also found a positive relationship between GPP and midge growth. A consumer–resource model fit to the experimental data showed a hump-shaped relationship between midge consumption rates and their somatic growth. In the model, predicted midge somatic growth rates were only positively associated with GPP when their consumption rate was below the value that optimized midge growth. Therefore, midges did not overexploit algae in the experiment. This work highlights the balance that consumers which depend on contemporaneous resource growth might have to strike between short-term growth and future food availability, and the benefits for consumers when they 'manage' their resources well.

Keywords: consumer–resource interactions, microalgae, Mývatn, primary consumers, prudent predation, *Tanytarsus gracilentus*

Introduction

A common assumption in consumer–resource interactions is that consumers benefit by consuming resources as rapidly as possible given the constraints imposed by the cost of capturing those resources (Schoener 1971, Rankin and López-Sepulcre 2005, Vuorinen et al. 2021). However, Slobodkin (1961, 1968) proposed the controversial notion that predators ought to manage their prey populations by consuming prey at a rate that allows for the long-term sustainability of both predator and prey populations.

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The ensuing debate this generated (Maynard-Smith and Slatkin 1973) largely focused on the scenario in which consumer and resource dynamics operate at similar timescales so that intra-generational dynamics of consumers and their resources are negligible (Murdoch et al. 2002). However, some consumers feed on the contemporaneous growth of their resources, either because they regularly consume part of a living organism (e.g. some grazing megaherbivores, Hempson et al. 2015, Bakker et al. 2016; and koinobiont parasitoids, Mackauer 1986) or they consume organisms that have relatively shorter generation times so that resource population dynamics occur within the lifespan of the consumer (e.g. aquatic fish and insects that feed on microalgae and bacteria, Sanchez and Trexler 2018, Lancaster and Downes 2018). If these consumers are territorial, in the general sense of controlling access to and relying on a limited pool of resources, then 'prudent predation' may improve survival and somatic growth of individual consumers (Munger 1984).

When consumers rely on a fixed pool of contemporaneously growing resources, an intermediate consumption rate likely maximizes their lifetime food availability. If the consumption rate is too high, consumers will too strongly reduce resource biomass early in their life, and there will not be enough resource growth to support further consumer growth as the consumer ages. However, if consumers have too low a consumption rate, they are 'leaving food on the table' and consequently give up growth potential, which is also maladaptive. The intermediate consumption rate that allows for the highest consumer growth is analogous to maximum sustainable yield, often used to guide fisheries management to maximize the acquisition of resources (fish) while not resulting in the collapse of the fishery (Russell 1931, Graham 1935, Post et al. 2002, Worm et al. 2009, Cahill et al. 2021). Because the rate at which individual consumers consume their own resources partly dictates the growth of the resources on which they depend, the consumers de facto are engaged in resource management.

Tanytarsus gracilentus (Diptera: Chironomidae) in Lake Mývatn, Iceland, depend on the contemporaneous growth of the resources in their close proximity. *Tanytarsus gracilentus* is a non-biting midge that primarily consumes epipelic algae and associated detritus occurring on and around silk tubes that they individually construct in the sediment (Ingvason 2002, Ingvason et al. 2004, Ólafsson and Paterson 2004). Individuals are thought to build a single silk tube which they spend the majority of their lifecycle as larvae (Chaloner and Wotton 1996, Ólafsson and Paterson 2004). Given the generally high nutrient and benthic light conditions in Mývatn, Fragilariaceae, the predominant epipelic algal group (Einarsson et al. 2004, McCormick et al. 2019), have a population doubling time on the order of days (Michel et al. 2006). This capacity for high primary production supports high rates of secondary production by *T. gracilentus* (Lindegaard and Jónasson 1979). As is common with benthic macroinvertebrate herbivores (Hillebrand 2002, 2009, Holomuzki et al. 2010), there is evidence that *T. gracilentus* can reduce the standing biomass of algae via consumption. Within a generation, there is strong evidence that somatic midge growth and development can be density dependent, which suggests that the per capita availability of resources can limit growth (Phillips et al. 2021a, Wetzel et al. 2021). Moreover, across generations, time series of both midge abundances and several metrics associated with their resource availability – wing lengths (Einarsson et al. 2002), pigments associated with diatoms in sediment cores (Einarsson et al. 2016), and isotopic signatures of midges (McCormick et al. 2022) – show fluctuations consistent with consumer–resource dynamics (i.e. lagged cycles).

In this study, we used a laboratory microcosm experiment to investigate the relationship between somatic growth of *T. gracilentus* and contemporaneous epipelic algal growth. We manipulated initial algal abundances in the presence and absence of midges to examine the effect of midge consumption on their resource abundance, and in turn the effect of resource abundance on midge somatic growth rates and survival. The experimental data allowed us to compare resource availability (measured as gross primary production, GPP) to the growth rates of midges over the course of the experiment. Finally, we used a mathematical model parametrized using the experimental data to determine how variation in consumption rates and maximum per capita algal growth rates influence the relationship between GPP and secondary production (midge growth) that is generated by the midge-algae consumer–resource interactions.

Material and methods

Study system and study organism

Mývatn is a large (37 km^2), shallow (mean depth = 2.5 m) lake in northeastern Iceland (65°40′N, 17°00′W). Springs along the eastern side of the lake supply 1.5, 1.4 and 340 g m^{-2} year^{-1} of nitrogen, phosphorous and silicon, respectively (Ólafsson 1979). The high nutrient inputs result in a highly productive ecosystem. Mývatn's primary production is mainly benthic, except during large cyanobacteria blooms that occur in some years (Einarsson et al. 2004, Phillips 2020, McCormick et al. 2021). The epipelic algal community in the habitat types where *Tanytarsus gracilentus* occurs is dominated by diatoms, especially those in the family Fragilariaceae (Einarsson et al. 2004, Ingvason et al. 2004, McCormick et al. 2019). At Mývatn, *T. gracilentus* can make up over 75% of the annual secondary production in some years (Lindegaard and Jónasson 1979). *Tanytarsus gracilentus* are holometabolous and have four discrete larval instars. Most of an individual's growth occurs between the second and fourth instar, when it resides in a silk tube that they construct in the sediment (Lindegaard and Jónasson 1979). These tubes boost primary production by providing a three dimensional substrate for epipelic algae to grow on (Phillips et al. 2019). The midges are generally bivoltine, with emergences in early June and in mid-July (Lindegaard and Jónasson 1979), and they enter diapause as larvae over winter (Ingvason et al. 2006).

Experiment

In August 2020, we established 100 microcosms in which we crossed the presence/absence of midge larvae with a gradient of algal abundance. Microcosms were constructed from 50 ml Falcon tubes (30 mm dia × 110 mm height) and included 20 ml of sediment. The microcosms were placed in incubation chambers that maintained temperature at ~ 12°C under high light with a 16:8 photoperiod reflecting field conditions. Inside the incubation chamber, the microcosms were housed in two water baths that allowed water to flow between microcosms in order to prevent anoxia (Supporting information). More details about the collection of sediment and midge larvae and about the construction of microcosms are found in the Supporting information.

We crossed the presence/absence of midges with 10 levels of initial algal abundance. We varied initial algal abundance using a serial dilution of algae-rich surface sediment with algae-poor sediment from 5–10 cm below the surface (Supporting information) (Poulíčková et al. 2008, Cantonati and Lowe 2014). The fractions of surface sediment used in the experiment were 1, 1/2, 1/4, 1/8, 1/16, 1/32, 1/64, 1/128, 1/256 and 0. We varied initial algal abundance rather than varying the growth rate of algae through manipulating light or nutrients because both can alter benthic algal community composition (Lange et al. 2011, McCormick et al. 2019), which could result in differences in food quality for midges (Danger et al. 2012). The midge treatment consisted of 20 s or third instar Tanytarsini (~28 000 ind. m^{-2}), which were subjected to a 24 h gut clearance period prior to their addition to the microcosms. This density is well below peak densities at Mývatn (500 000 ind. m^{-2}; Thorbergsdóttir et al. 2004) and therefore is unlikely to artificially alter the consumption rate of larvae (Hillebrand 2009). Each combination of midge treatment and initial algal abundance had five replicates. The contrast between the presence/absence midge treatment allows for evaluating the effects of midge consumption on the algal community, while the contrast between the initial algal abundance treatments allows for evaluating the effect of resource availability on midge growth.

We ran the experiment for 22 days which is roughly the length of the growing phase of larval midges from the second instar to pupation during the summer generation (Lindegaard and Jónasson 1979, Phillips et al. 2021a, Wetzel et al. 2021). After two weeks and at the end of the experiment, we measured GPP under light saturation, which served as a measure of food availability for midges. Following both incubation periods, we destructively sampled a random subset of microcosms from each treatment (two from each midge algae combination on day 14 and the remaining three on day 22) to determine the effects of the initial algal abundance on midge survival and growth.

Algal productivity

Beginning on days 11 and 20 of the experiment we conducted dissolved oxygen (DO) incubations in light and dark to measure the productivity of the algal community in each microcosm. These incubations allowed us to measure the GPP of the sediment under the commonly used assumption that respiration is the same in the dark as it is in the light (Staehr et al. 2010, Weathers et al. 2012). The consumption of oxygen in the dark reflects respiration by heterotrophs and autotrophs (ER). The change in DO in the light is the net ecosystem production (NEP), which includes both the generation of oxygen through photosynthesis and the consumption of oxygen through respiration. GPP is therefore the sum of NEP and ER.

We calculated GPP using measurements of ER and NEP for all microcosms on both incubation dates. We measured DO using a handheld optical DO probe (ProODO, YSI). During the incubations, we sealed the microcosms with airtight caps. Because the probe displaced water, we added oxygen-saturated room temperature water to the microcosms until there was no air in the sealed microcosms. The change in DO concentration was calculated accounting for the volume and DO concentration of the water added. The light incubations lasted roughly 24 h and the dark incubations lasted roughly 11 h to ensure a detectable signal of NEP and ER across all algal treatments while avoiding supersaturation and anoxia. We treated GPP as a metric of algal abundance. This was necessary because we sieved microcosms to collect midges and therefore could not use other metrics such as chlorophyll-a.

Midge survival and growth

During the experimental setup, we collected 60 additional midges that were also subjected to the 24 h gut clearance period and then sampled (on day 0) to measure starting abundance (i.e. to account for mortality during the 24 h gut clearance period), instar, and confirm species identity. On day 14, we destructively sampled two randomly selected replicates from each treatment (40 total) and on day 22 sampled the remaining three replicates (60 total). For simplicity, we refer to sampling event for both the incubation and the midge samples as days 14 and 22. To collect the midges, we sieved all microcosms through 125 μm mesh and transferred all live midges present from each microcosm into 70% ethanol, where they were identified and counted. Additionally, we measured their head capsule width to determine instar and measured the body length of each individual midge. We used head capsule widths collected during routine monitoring of the Tanytarsini at Mývatn between 2013 and 2020 to delineate instar head widths (Supporting information).

For each microcosm that was stocked with midges, we estimated the average individual mass and growth rate of midges, expressed as the change in ash free dry mass (AFDM) per day. We converted all individual body lengths into AFDM using the empirical relationship developed for *T. gracilentus* at Mývatn (Table 21 in Lindegaard and Jónasson 1979), which allowed us to estimate the average mass for midges in each microcosm. Because we did not mark and repeatedly measure individual midges, we could not calculate growth rates for each individual. Therefore, we estimated the mean and uncertainty in individual growth rates for each treatment using a bootstrapping procedure (Brey 1990). We resampled the individual-level AFDM data for each treatment on days 0, 14 and 22, 1000 times using *sample_n* in 'dplyr' ver. 1.0.6 (Wickham et al. 2021) in R (www.r-project.org). From these bootstrapped data, we calculated the mean and standard error in the somatic growth rate between day 0 and days 14 and 22 in each treatment.

Data analysis

To assess the effect that midges had on primary production (GPP), we used linear regression models. We included a term for initial algal abundance as a continuous predictor ranging from 0 (no surface sediment) to 1 (ambient algal abundance, all surface sediment). Initial algal abundance was log transformed to avoid problems with leverage due to the serial dilution. We used 0.002, which is half of the lowest value, as the value for the microcosms containing no surface sediment. We included water bath identity (two levels) as a fixed effect. Rather than fit a single model with a three-way interaction (incubation date × midge treatment × initial algal abundance), we fit the days separately to aid in interpretation and to avoid heteroskedasticity since the variance in the residuals differed between incubation days.

To examine the effect of initial algal abundance on midge survival and growth, we fit regression models with two different response variables: the number of midges in a microcosm and midge body length. We used a quasi-Poisson generalized linear model (GLM) to analyze the number of midges in a microcosm. This model included fixed effects for initial algal abundance (log transformed), midge treatment, the interaction between initial algal abundance and midge treatment, and a factor for the water bath. We also fit a linear mixed effects model (LMM) to determine the effects of the sediment and midge treatments on the length of the individual midges collected. The fixed effects for this model were the same as described above. However, the LMM differed in that it included a microcosm level random effect, as there were multiple measurements (i.e. midges) per microcosm. All models were fit separately for the two sampling events.

To compare primary production and midge growth (secondary production), we converted them to comparable units. Primary production was converted from oxygen production to carbon incorporation (μg C cm^{-2} day^{-1}) assuming a photosynthetic quotient of one (Thorbergsdóttir and Gíslason 2004, McCormick et al. 2021). We converted average somatic midge growth from AFDM into μg C ind^{-1} day^{-1} assuming that AFDM was 50% carbon (Benke et al. 1999). Then we fit a measurement error model to relate the two. The model is analogous to a simple linear regression with average primary production as the response variable and midge growth as the sole explanatory variable. However, unlike traditional linear models, which assume uncertainty in only the response variable, our measurement error model assumed uncertainty in both the response and the explanatory variable. Additionally, the measurement error model that we used accounted for the different uncertainties associated with each estimate of primary production and average midge growth for each treatment (Ives et al. 2007).

We conducted all analyses in R ver. 4.1.2, (www.r-project.org). We fit linear regression models using the *lm* function in the 'stats' package, GLMs using the function *glm* in the 'stats' package (www.r-project.org), and linear mixed effects models using *lmer* in the 'lme4' package ver. 1.1-27.1 (Bates et al. 2015). We calculated the statistical significance of the effects in the LM and GLM with t-tests implemented using the *summary* function in the 'stats' package. We calculated p-values in the LMM using type III Wald F tests implemented using the *Anova* function in the 'car' package ver. 3.0-12 (Fox and Weisberg 2019). For all models, to assess the significance of the main effects with type II tests, we dropped all interactions. The measurement error model was fit using the *pgls.Ives* function in the 'phytools' package ver. 1.0-1 (Revell 2012).

Model

The experiment yielded an empirical relationship between the contemporaneous resource availability and the somatic growth of midges from second through fourth instars. Theoretically, we expect this relationship to depend on the midge consumption rate, with intermediate consumption rates leading to the greatest midge growth. Midge consumption rates, however, could not be experimentally manipulated. Therefore, we fit a model of algal and midge growth to our experimental data to investigate the expected consumer–resource interactions under different midge consumption rates.

We designed a simple model, because a more biologically detailed model would be difficult to statistically fit to the data. The model is discrete-time version of a Lotka–Volterra predator–prey model with prey density-dependent self-limitation (Edelstein-Keshet 1988) given by a coupled pair of difference equations:

$$\begin{aligned} X_t &= e^r X_{t-1}^b - aX_{t-1}Y_{t-1} \\ Y_t &= Y_{t-1} + caX_{t-1}Y_{t-1} \end{aligned} \tag{1}$$

Here, X_t is resource biomass available to an individual consumer on day *t*. Because we did not collect both midges and sediment from the same microcosms, we do not have direct measures of algal biomass. Instead, we let X_t be the photosynthetic potential of algae, that is, the rate of photosynthesis of the algae under saturating light conditions, matching the conditions of the experiment. Because GPP depends on resource biomass, biomass-specific growth rates and irradiance, GPP under saturating light conditions gives a functional measure of biomass that is directly related to algal growth rates. We further assume that microcosms are homogenous with respect to these measurements, such that the areal rates of GPP under saturating light reflect the GPP of algae in the vicinity of an individual midge. Y_t is the average mass of an individual midge on day *t*.

In the model, the rate at which the photosynthetic potential of algae increases is determined by its maximum per capita growth rate r and density dependence (e.g. self-shading and nutrient limitation) b. When $b < 1$, per capita algal growth diminishes with increasing X_t. Algae are consumed by midges with a biomass-specific consumption rate a, and the efficiency with which algae are converted into midge biomass is scaled by c. The conversion efficiency c is equivalent to the midge gross production efficiency, which is the fraction of biomass consumed that is not egested, excreted, or respired (Benke and Huryn 2017). In the model, the biomass-specific consumption rate of midges is fixed, but total consumption depends upon their biomass Y_t so that larger midges consume more algae (e.g. to support higher metabolic costs).

To fit the model to data from the microcosm experiment, the only available measure of algal photosynthetic potential (X_t) at the start of the experiment was chlorophyll-a concentration, which is highly correlated with GPP under light saturating conditions (McCormick et al. 2021). Because we had two different measurements (chlorophyll-a and GPP), they were standardized separately by dividing by their respective means, and we included a fitted parameter g to convert between scaled chlorophyll-a concentration and scaled GPP. Y_t was fit to average individual mass of midges in each microcosm standardized by the grand mean across all treatments and sampling days. Therefore, both X_t and Y_t are dimensionless. Because the observed variance of the residuals scaled with the log of X_t and Y_t, we fit the model by minimizing the sums of squared residuals between log observed and log predicted values using the *optim* function in the 'stats' package in R (www.r-project.org).

We simulated the fitted model to explore the relationship between resource supply and consumer growth as it is modified by changes in the algal growth rate, r, and the midge consumption rate, a. We used the same initial algal abundances and average starting midge biomass as used in the experiment and then simulated X_t and Y_t for 22 days varying either r (set to 0.5, 1.5 or 3) or a (from 0 to 0.4). We report values of light saturated GPP on a given day, X_t, average midge mass, Y_t, and average daily midge growth rates, $(Y_t - Y_{t=0})/t$, converted back to original units.

Results

Experiment

Data from the experiment on algal and midge growth consist of samples at the initial time point and at days 14 and 22. On day 14, GPP was positively related to initial algal abundance and unrelated to the presence of midges, and the interaction between initial algal abundance and midge presence was nonsignificant (Fig. 1A, Table 1). In contrast, there was a significant initial algal abundance by midge interaction on day 22, with the positive association between GPP and initial algal abundance only in the presence of midges. When midges were absent, there was no longer a difference in GPP among microcosms with different initial algal abundances.

Midges were more abundant and larger in microcosms that had higher initial algal abundance. We found more live individuals in microcosms with higher initial algal abundance on both day 14 and 22 (Fig. 1B, Table 2). Overall mortality across all microcosms was approximately 27% after accounting for the low mortality during the 24h gut clearance period (12%, 7/60). Sixty-four individuals (10% of the total number of midges collected at the end of the experiment) were found in microcosms that were not stocked with midges, while two microcosms (both from the microcosms with the highest initial algal abundance) had more than the 20 individuals with which they were stocked (Fig. 1B). Together, these results indicate that there was some movement of individuals between the microcosms. On both day 14 and 22, average midge body lengths were positively associated with initial algal abundance (Fig. 1C, Table 3). On day 14, body lengths were close to those of midges used to stock the experiment (Fig. 1C). Across both sampling events, we found larger midges in microcosms with higher initial algal abundance (Fig. 1C, Table 3). Similar patterns were seen for midge development rates (the proportion of individuals that progressed past 2nd instar; Supporting information).

Estimated average individual midge growth rates were positively associated with algal primary production rates on the two incubation days (Fig. 2). For some microcosms with low initial algal biomass, average midge growth was negative, which could be the result of reductions in size due to starvation or disproportionate mortality of larger individuals in resource-limited microcosms.

Model

Using our consumer–resource model, we assessed how different midge consumption rates are expected to change the relationship between primary production and midge growth. We fit the model to the data (Supporting information), which yielded the parameters in Table 4. The model showed a hump-shaped relationship between the midge growth rate and the midge consumption rate (Fig. 3). This occurred because low consumption rates led to low use of available resource, while high consumption rates reduced algal abundance early in the simulations, suppressing subsequent resource supply (Fig. 4). The consumption rate estimated from the observed data was below the rate that would have optimized midge growth. Therefore, the model implies that midges could have maximized their short-term growth over the course of the experiment with a higher consumption rate.

Although the experiment showed a positive relationship between primary production and midge growth (Fig. 2), the model shows that the relationship could potentially be very different. In the model, increasing biomass-specific consumption rate a and maximum per capita algal growth rates r resulted in a negative relationship between midge growth and primary production on day 22 (Fig. 5). Increasing the per capita algal growth rate increases the rate of midge biomass accumulation. As time progresses in the simulations, the accumulated midge biomass becomes higher than algal

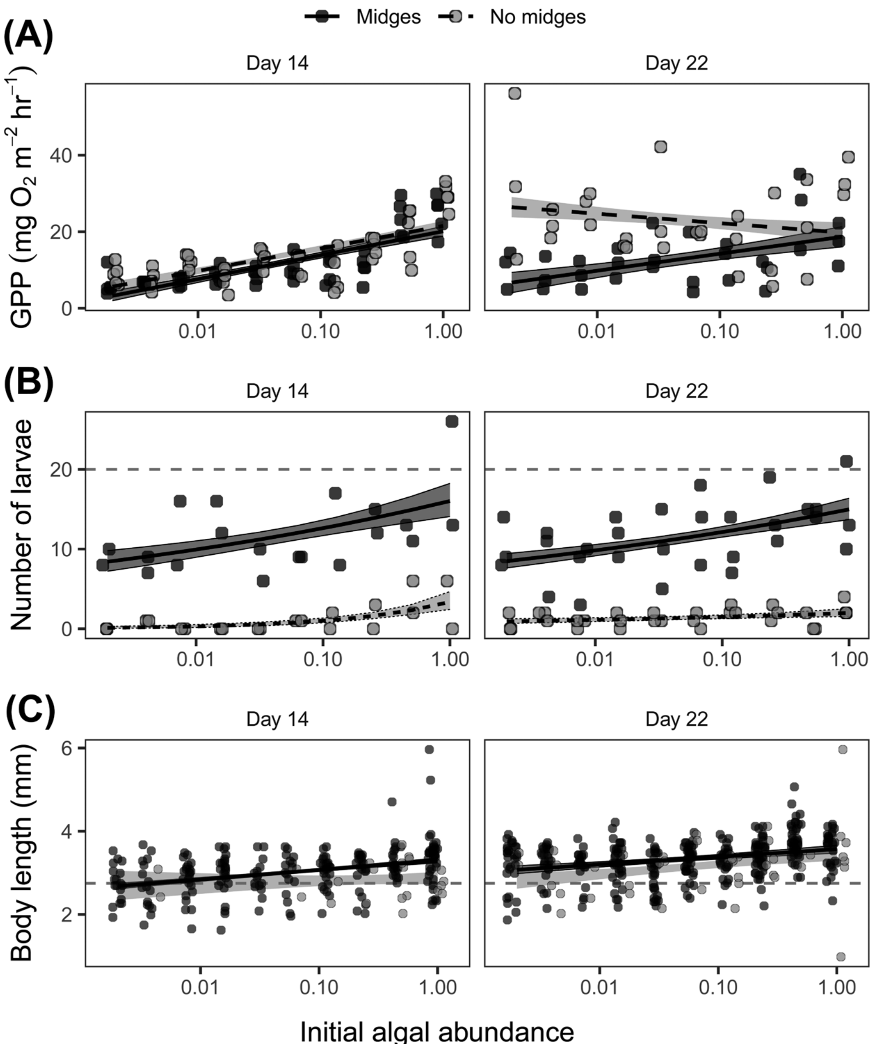

Figure 1. (A) GPP increased with initial algal abundances on day 14, but not on day 22 in the absence of midges. (B) Higher numbers of live midges occurred in microcosms that were stocked with midges and in microcosms which received higher initial algal abundances. (C) higher initial algal abundance was associated with larger midges. Points show microcosms (A and B) or individual midges (C) and are jittered horizontally for legibility. Lines show model fits and shaded regions show 1 standard error around the estimate. Dashed horizontal lines show starting numbers of midges (B) and average initial body length (C). Note the x axis for all figures is on a log scale.

Table 1. Effects of sediment and midge treatments on gross primary production (GPP) on days 14 and 22 of the experiment with and without interactions (type III and type II tests, respectively). Initial algal abundance was the proportion of surface sediment used for microcosms and was log transformed.

		Type III		Type II	
	Estimate	t	p	t	p
Day 14					
Initial algal abundance	2.551	7.353	<0.0001	10.780	<0.0001
Midges	−1.393	−0.768	0.444	−1.956	0.053
Water bath	−1.266	−1.293	0.199	−1.295	0.199
Initial algal abundance × Midges	0.164	0.334	0.739		
Day 22					
Initial algal abundance	−1.07	−1.482	0.144	0.809	0.422
Midges	−1.099	−0.292	0.771	−4.860	<0.0001
Water bath	−9.539	−4.677	<0.0001	−3.984	0.0002
Initial algal abundance × Midges	2.994	2.921	0.005		

Table 2. Effects of sediment and midge treatments on the number of midges present in a microcosm. Data were analyzed using a quasi-Poisson GLM fit to days separately, and models were fit with and without interactions (type III and type II tests, respectively). Initial algal abundance was the proportion of surface sediment used for microcosms and was log transformed.

		Type III		Type II	
	Estimate	t	p	t	p
Day 14					
Initial algal abundance	0.526	3.260	0.002	3.348	0.002
Midges	1.560	4.409	<0.0001	8.617	<0.0001
Water bath	0.237	1.615	0.115	1.858	0.071
Initial algal abundance × Midges	−0.422	−2.538	0.016		
Day 22					
Initial algal abundance	0.124	1.636	0.108	3.862	0.0003
Midges	2.023	7.709	<0.0001	13.544	<0.0001
Water bath	−0.172	−1.728	0.090	−1.807	0.076
Initial algal abundance × Midges	−0.032	−0.402	0.689		

growth can support and X_t decreases (Supporting information). When algal abundances are initially high, the point when this occurs is sooner, generating the negative relationship between projected primary production and midge growth (Fig. 5). While attack rates above the optimum are associated with a reduction in midge growth, increases in resource growth rates are always associated with increased midge growth rates as seen by the changes in scale of the vertical axes of the panels in Fig. 5.

Discussion

In this study, we explored the relationship between a consumer (the midge, *T. gracilentus*) and its continuously growing resources (epipelic algae). We performed a microcosm experiment where we manipulated the initial abundance of algae and presence/absence of midges. We found that midge consumption controlled primary production. We also found that higher initial algal abundances were associated with higher abundances and faster growth rates of midges. Our experimental results generated a positive relationship between primary production and midge growth. Using a model parameterized by the experiment, we found that the positive association between primary production and midge growth was not inherent and only occurred when midge consumption was below the value that maximized their somatic growth. Increasing the consumption rate or the algal growth rate resulted in a negative association between midge growth and primary production. This detailed exploration of midge–algal interactions shows how high consumption rates can result in lower somatic growth for consumers feeding on contemporaneously growing resources.

Our experimental results show that higher lifetime resource availability supports higher *T. gracilentus* somatic growth. In previous experiments, reducing per capita resource availability by increasing midge density resulted in fewer emerging *T. gracilentus*, higher mortality rates, and smaller larvae (Phillips et al. 2021a, Wetzel et al. 2021). Additionally, reductions in per capita algal growth rates via shading resulted in lower midge survival, growth, and emergence (Wetzel et al. 2021, Phillips et al. 2021b). Studies on other midge species that have manipulated food quantity have shown a similar response (Rasmussen 1985, Macchiusi and Baker 1992, Vos et al. 2000, Péry et al. 2002, Hooper et al. 2003, Doi et al. 2007); however, these studies generally used non-growing food (e.g. fish flakes), which consumers could not 'manage.' One study on snails (Cross and Benke

Table 3. Effects of sediment and midge treatments on the body length of midges (mm). Data were analyzed using a linear mixed effects model with microcosm identity as a random effect. Models were fit to days separately. p-values were calculated using type III Wald F tests with Kenward Roger degrees of freedom for the models with interactions and type II Wald F tests with Kenward Roger degrees of freedom for the reduced models. Initial algal abundance was the proportion of surface sediment used for microcosms and was log transformed.

		Type III		Type II	
	Estimate	$F_{ndf,ddf}$	p	$F_{ndf,ddf}$	p
Day 14					
Initial algal abundance	0.028	$0.163_{1,213.492}$	0.686	$33.640_{1,12.511}$	<0.0001
Midges	0.426	$6.954_{1,52.169}$	0.011	$7.100_{1,66.701}$	0.0097
Water bath	−0.048	$0.486_{1,13.051}$	0.498	$0.646_{1,13.636}$	0.435
Initial algal abundance × Midges	0.071	$0.986_{1,174.214}$	0.322		
Day 22					
Initial algal abundance	0.104	$5.310_{1,134.365}$	0.023	$15.021_{1,41.093}$	0.0004
Midges	0.124	$0.478_{1,71.494}$	0.592	$3.7431_{,88.798}$	0.056
Water bath	0.033	$0.136_{1,41.983}$	0.715	$0.080_{1,42.552}$	0.779
Initial algal abundance × Midges	−0.024	$0.213_{1,84.949}$	0.645		

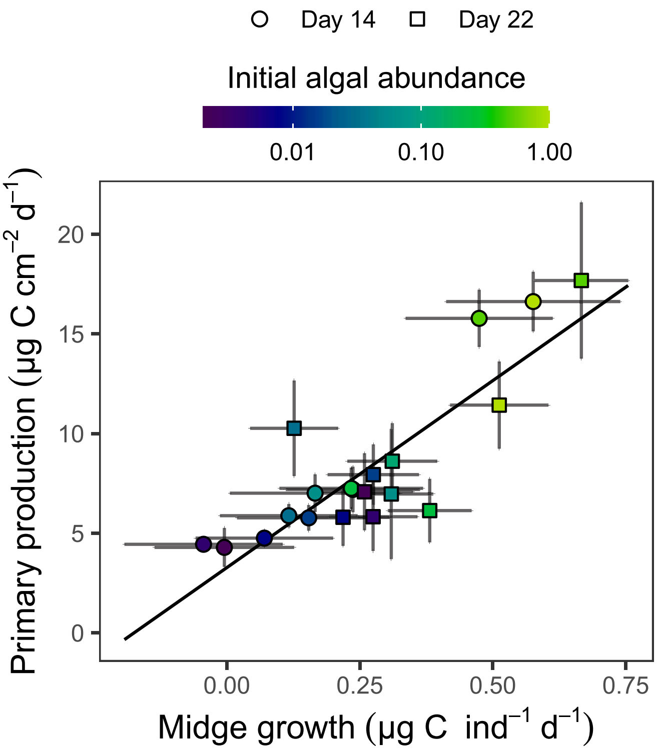

Figure 2. Primary production and the average somatic growth rate of midges in the experiment were positively related. Variation in primary production was driven by changes in intial algal abundance. Vertical and horizontal bars show one SE. The line shows the fit of the measurement error model.

2002) manipulated initial densities of growing periphyton and found higher periphyton density increased snail growth, similar to our results.

We found that feeding by midges suppressed the accumulation of algal biomass. In the absence of midges, primary production did not differ between microcosms with different initial algal biomass by the end of the experiment. However, in the presence of midges, primary production still reflected initial algal biomass. Therefore, even the low densities of *T. gracilentus* used in the experiment (compared to peak natural densities) suppressed the growth of the algae under high light conditions. This result is consistent with studies on invertebrate grazers in streams showing that grazers can slow the accumulation of algal biomass when algal biomass is initially low, such as following scouring events (Lamberti et al. 1989, DeNicola et al. 1990, Wellnitz and Rader 2003, Wellnitz and Poff 2006). However, we found that algae had the capacity to grow rapidly in the absence of midges, such that GPP no longer differed between microcosms that had dramatically different starting algal biomass within the lifespan of a midge.

The reciprocal interactions between midges and algae generated a positive relationship between primary production and midge growth during the experiment. However, our model shows that consumer growth is not necessarily positively related to primary production. This occurs because midge biomass is accumulated over time, whereas the turnover of algae can be rapid. Early increases to midge biomass, either through increases in consumption rates or increases in the growth rate of algae, resulted in overexploitation. Our result that increased algal productivity resulted in overexploitation is similar to the paradox of enrichment (Rosenzweig 1971), where increased prey production results in the collapse of the prey population by boosting predator production. A positive relationship between midge biomass and instantaneous rates of primary production in the model only occurred when resource growth rates exceeded the removal rate by consumers. Therefore, our estimated parameters suggest that under low midge density and high light conditions of the experiment, midges did not overexploit their resources.

Our finding that midges suppressed but did not overexploit algae may partly help to explain how midges are able to undergo dramatic increases in population abundance. Following periods of low abundance, the midge population abundance can increase by over 10-fold per generation (Gardarsson et al. 2004). This high population growth may be related to midges' capacity to 'manage' their resources well. In fact, midges and other primary consumers feeding on contemporaneously growing resources often boost the rates at which their resources grow. *Tanytarsus gracilentus* build silk tubes which appear to increase algal growth rates by alleviating light limitation (Phillips et al. 2019), and this can increase the survival of midges (Phillips et al. 2021a). Other aquatic insect herbivores also build tubes that increase algal production (Pringle 1985, Ings et al. 2010, Tumolo et al. 2019). Bioturbation by detritivorous midge species can enhance microbial production (Hölker et al. 2015, Baranov et al. 2016, Samuiloviene et al. 2019). Furthermore, aquatic primary consumers often increase dissolved nutrient availability or the rate of nutrient cycling which can increase resource growth rates (André et al. 2003, Ings et al. 2012, Mooney et al. 2014, Hölker et al. 2015). Thus, many consumers that rely on contemporaneous production may modify the environment experienced by resources in ways that improve their resource supply and enhance their own growth.

Table 4. Parameters of the consumer–resource model (Eq. 1) estimated from the experimental data.

Parameter	Definition	Estimate
r	Maximum per capita growth rate of algae	0.17
b	Density dependence of algae	0.93
a	Consumption rate of midges on algae	0.044
c	Conversion factor of algal photosynthetic potential to midge biomass	0.17
G	Conversion factor to relate scaled GPP to scaled chlorophyll-a	0.21

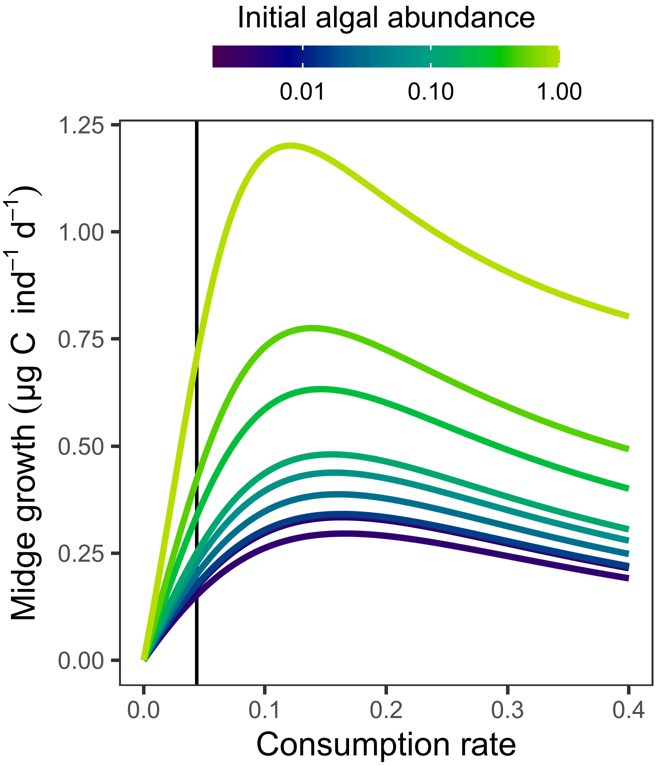

Figure 3. In the model fitted to experimental data, midge growth is maximal at intermediate consumption rates for all initial algal abundances. The x-axis shows the consumption rate of midges on algae (parameter *a*), and the y-axis shows the projected daily midge growth. Lines are colored by initial algal abundance which generated variation in X_t at day 0. The vertical line shows the consumption rate estimated from the experimental data. Parameters from the fitted model are in Table 4.

Although our experiment was not designed to study midge movement, we found evidence that some *T. gracilentus* moved between microcosms. This movement appeared to be associated with resource availability, as microcosms with higher initial resources were those that tended to increase in midge density. This observation is consistent with theory and empirical evidence suggesting that consumers ought to move when the cost of acquiring local resources exceeds that of moving to a new habitat patch (Pyke 1984, Morris 2006, Mueller and Fagan 2008, Abrahms et al. 2020). The cost of habitat abandonment is likely to be much higher for consumers that engage in ecosystem engineering (Hershey 1987, Wiley and Warren 1992). Lotic *Tanytarsus* were not observed to abandon tubes unlike other tube-building midges in behavioral studies, which is presumably because their robust tubes require a higher investment than the other taxa studied (Chaloner and Wotton 1996). Given the relatively high cost of tube building and the poor swimming ability of later instar midges which makes them susceptible to predators (Davies 1976), we suspect that movement of later instar *T. gracilentus* is rare in Mývatn. Therefore *T. gracilentus* individuals that settle in a higher quality habitat patch and consume resources at an optimal rate are likely to have higher survival and somatic growth than those that overexploit their resources and rely on movement.

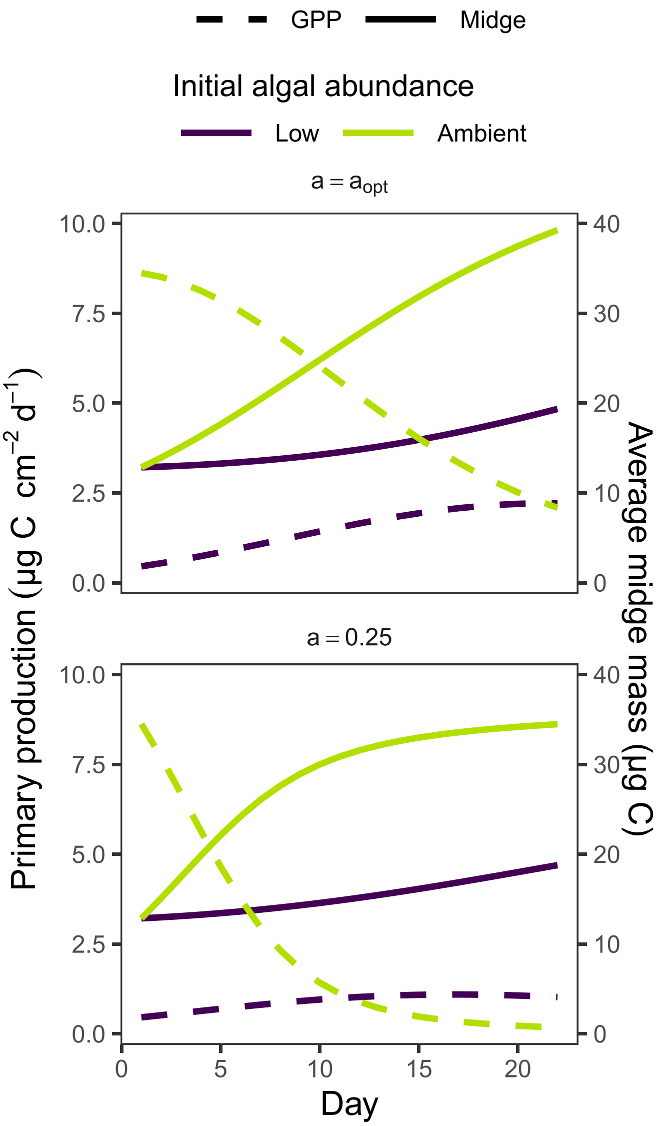

Figure 4. From the model, dynamics of midge mass (solid) and GPP (dashed) over the attack rates below, above, and at the optimum. Only the highest and lowest initial algal abundances are shown to aid in visualization. Unless stated, all parameters are as in Table 4.

In our experiment, midge densities were moderate and light levels were high, leading to moderate consumption rates and high algal primary production. Therefore, even though midge consumption rates were lower than algal growth rates in the experiment, this might not always be the case under natural conditions. The factors limiting resource growth may vary over time in dynamic environments (Meserve et al. 2003). When density-independent factors limit the growth of resources, a moderate consumption rate would not support higher resource growth. Similarly, when consumers are unable to control their territory, as might be the case when conspecific densities are very high, individuals with high consumption rates are favored (Rankin and López-Sepulcre 2005). In Mývatn, cyanobacterial blooms can reduce all epipelic algal production for weeks (McCormick et al. 2021),

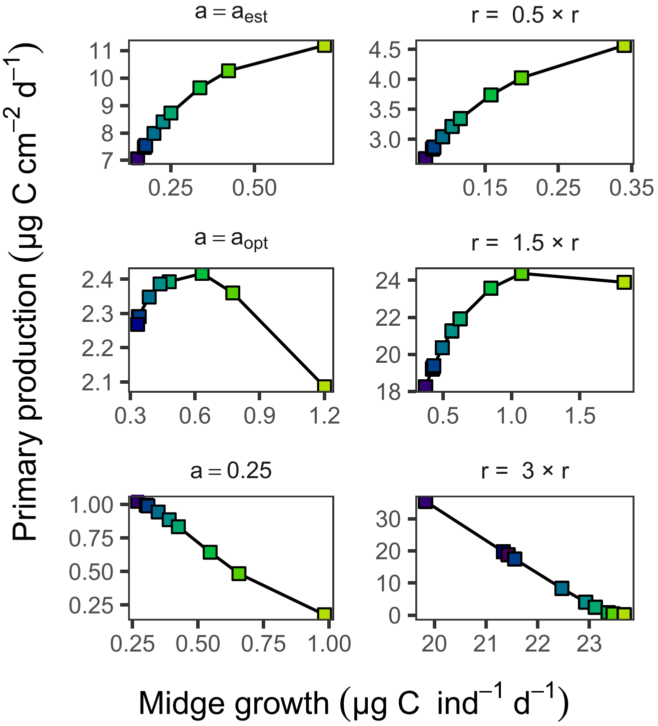

Figure 5. From the model, projected patterns of average daily midge growth ($(Y_t - Y_{t=0})/t$) and primary production (X_t) under different resource growth rates and initial resource availability (set to those values used in the experiment) on day 22. Initial consumer biomass ($Y_{t=0}$) for all treatments was equal. Lines connect points across initial resource biomasses. Unless stated, all parameters are as in Table 4.

and midge densities can become more than ten times higher than the experimental densities (Lindegaard and Jónasson 1979, Thorbergsdóttir et al. 2004). Under these conditions, it is likely that *T. gracilentus* will overexploit their resources, and they may need to move or rely on detrital resources more heavily. In fact, an analysis relating midge production to primary production over 11 years at Mývatn shows several periods where midge consumption could not be supported by algal growth, and the sediment shows coincident declines in the quantity of detritus (Botsch 2023).

Consumers that depend on the growth of their resources must balance their immediate consumption of resources against resource growth and future abundance. Our experiment with *T. gracilentus*, in conjunction with a model fit to the experimental data, gave evidence that midges do not inherently overexploit their resources. Consumers often employ behaviors that mitigate the likelihood of overexploitation of their resources (Vuorinen et al. 2021), such as enhancing resource growth rates through ecosystem engineering (Jones et al. 1994) and abandoning low-resource habitat patches (Power 1984, Wiley and Warren 1992, Munubi et al. 2018), both of which we observed by *T. gracilentus*. How consumers manage their resources in a dynamic environment may shape their somatic growth rates and subsequently their population dynamics.

Speculations

It is tempting to infer that evolution favors resource management among territorial consumers that rely on contemporaneous growth. If consumption rates are heritable and the conditions favor resource management, then it is conceivable that populations may evolve an intermediate consumption rate (‘prudent predation’). However, many other factors contribute to an individual’s consumption rate that may also result in an intermediate consumption rate (Vuorinen et al. 2021, Gutiérrez Al-Khudhairy and Rossberg 2022). Whether a happy accident or the product of evolution, individuals that manage their resources well are likely to experience higher rates of somatic growth and survival.

Acknowledgements – We thank Árni Einarsson for scientific insights and support at the Mývatn Research Station. We also thank Emily Stanley, Claudio Gratton, Volker Radeloff and John Orrock for providing feedback on the manuscript.
Funding – Support for this research was provided by Árni Einarsson and the Mývatn Research Station. This work was funded by the National Science Foundation (DEB-2134446 to ARI) and an NSF Graduate Research Fellowship to JCB (DGE-1747503).

Author contributions

Jamieson C. Botsch: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Writing – original draft (lead); Writing – review and editing (lead). **K. Riley Book**: Conceptualization (supporting); Investigation (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Joseph S. Phillips**: Conceptualization (supporting); Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Anthony R. Ives**: Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from Zenodo : https://doi.org/10.5281/zenodo.7250504 (Botsch et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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