# The relationship between primary production and primary consumer growth when consumers rely on concurrent resource growth

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Abstract (200 words)

Some consumers live much longer than their resources, and these consumers may depend on the contemporaneous growth of the resources. They ought to grow fastest when the population growth rate of the resource species is maximized. As larvae, the midge *Tanytarsus gracilentus* feed on microalgae that grow on tubes they construct in the sediment. We performed a microcosm experiment in which we manipulated initial algal abundance and the presence of midge larvae. We found that midges slowed the accumulation of algal biomass and that higher gross primary production rates (GPP) were associated with faster somatic midge growth. To further investigate these feedbacks, we fit a consumer-resource model to the experimental data. The model shows highest somatic midge growth rates when consumption is moderate. By altering midge consumption rate and per capita algal growth rates in silico, we found that midge growth rates were only positively associated with GPP when midge consumption was below the optimum and midge consumption did not exceed algal growth. This work highlights the challenges facing consumers feeding on continuously growing resources, how the balance of consumption and resource growth shapes patterns of biomass, and how consumers can overcome these constraints to achieve high rapid population growth.

**Abstract** (199)

Some consumers depend on the contemporaneous growth of the resources they feed on. For example, *Tanytarsus gracilentus* midges feed on silk tubes that they construct in the sediment. Because the midge generation time is much longer than that of algae, their growth may be supported contemporaneous algal growth. This implies that an intermediate consumption rate maximizes midge somatic growth: a low consumption constrains growth, whereas too high consumption reduces algal abundances, limiting their food supply. We investigated the relationship between somatic midge growth and primary production (GPP) in an experiment manipulating the initial abundance of algae in microcosms with and without midges. We found a positive relationship between GPP and midge growth. We further investigated the feedbacks between midge consumption and GPP by fitting a consumer-resource model to the experimental data. The model shows the expected hump-shaped relationship between midge consumption rates and their growth. Altering midge consumption rates and per capita algal growth rates resulted in different patterns of projected midge growth and GPP. The positive relationship between instantaneous primary production and midge growth seen in the experiment suggest that they did not overexploit algae. This work highlights the challenges faced by consumers feeding on contemporaneously growing resources.

# Introduction

The generation time of many consumers greatly exceeds the lifespan of their resource species. Examples include aquatic insects and fish that primarily consume microalgae or bacteria (Sanchez and Trexler 2016, Lancaster and Downes 2018). When consumers are much longer lived than their resources, the relevant availability of resources for consumer growth is not only standing resource biomass, but also the production of new resource biomass over the lifespan of the consumer (Odum 1968, Polis and Strong 1996), which we refer to as resource supply. Limited resource supply can have large consequences for the population dynamics of consumers, because it can result in reductions in abundance through increased mortality rates and reduced somatic growth rates (Lawton et al. 1980, Agnew et al. 2002, Hooper et al. 2003). Somatic growth rates are tightly coupled to population growth rates because they are often related to development time and individual body size at maturity (Nylin and Gotthard 1998). Lower resource supply can result in longer development times (fewer generations per unit time) and smaller mature individuals, which tend to be less fecund within a given species (Honěk 1993, Koskela et al. 1998, Kingsolver and Huey 2008). Despite its potential importance, relatively few studies have explicitly considered the role of contemporaneous resource supply in driving growth of a longer-lived consumer.

The balance between consumption and resource supply is likely to be an important determinant in successful consumer somatic growth. Per capita population growth rates are often fastest at lower population densities, because high densities result in high intraspecific competition for limiting resources (Ricker 1954, Arditi and Ginzburg 1989, Sibly et al. 2005). Because longer-lived consumers are supported by the supply of resources over their lifespan, these consumers ought to have the fastest growth rates when the resource species is at moderate densities. If densities of the resource species are too low, there may not be enough biomass to support consumer growth, despite high per capita resource growth rates. If densities of the resource species are too high, consumers are leaving food on the table and per capita resource growth rates are lower due to high interspecific competition of the resource species. Therefore, a consumer should be able to grow the fastest when its consumption rate maximizes its resource supply. This is analogous to the concept of maximum sustainable yield, often used to guide fisheries management (Russell 1931, Graham 1935, Post et al. 2002, Worm et al. 2009, Cahill et al. 2021). However, unlike anglers, it is not necessary that consumers knowingly employ adaptive management strategies to ensure sustainable harvest of their resources.

Both somatic and population growth by *Tanytarsus gracilentus* (Diptera: Chironomidae) in Lake Mývatn, Iceland, depend on the contemporaneous growth of their resources. *T. gracilentus* is a non-biting midge that has two generations a year and primarily consumes epipelic algae and its associated autochthonous detritus (Ingvason 2002, Ingvason et al. 2004). Given the generally high nutrient and benthic light conditions in Mývatn, Fragilariaceae, the predominant epipelic algae in Mývatn (Einarsson et al. 2004, McCormick et al. 2019), likely 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). Additionally, reductions in primary production rates through shading slows midge development (Wetzel et al. 2021). Across generations, time series of both midge abundances and a variety of 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. in press)-- show fluctuations consistent with consumer resource dynamics.

In this study, we used a laboratory microcosm experiment to relate somatic growth of *T. gracilentus* to contemporaneously growing epipelic algae. We focus on somatic growth rate of midges because of its connection to midge fecundity (Xue and Ali 1994) and because the timescale of somatic growth connects *T. gracilentus* with the population growth of algae. We manipulated initial algal abundances in the presence and absence of midges to examine the effect of midge consumption on their resource supply. We also measured somatic growth rates and survival of midges across a range of initial algal densities to evaluate the effect that balance has on midge growth. Using these metrics, we compared instantaneous measures of resource supply (gross primary production; GPP) to the growth rates of midges. Finally, we used a mathematical model parametrized from the experiment to determine how variation in consumption rates and maximum per capita resource growth rates determine the relationship between instantaneous measurements of primary production and consumer growth that is generated by consumer-resource interactions.

# Methods

## Study System and Study Organism

Mývatn is a large (37 km2), shallow (mean depth = 2.5 m) lake in northeastern Iceland (65°40’N 17°00’W). Springs along the eastern side of the lake carry 1.5, 1.4, and 340 g m-2y-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 *T. 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). *T. gracilentus* are holometabolous and have four discrete larval instars. Most of their growth occurs between the second and fourth instar, when they reside in silk tubes which they construct in the sediment (Lindegaard and Jónasson 1979). These tubes appear to boost primary production (Phillips et al. 2019). They are generally bivoltine, with emergences in early June and in mid-July (Lindegaard and Jónasson 1979) and enter diapause over winter (Ingvason et al. 2006).

## Experiment

In August of 2020, we established 100 microcosms in which we manipulated the presence of midge larvae (midge treatment) and algal abundance at the sediment-water interface (initial algal abundance). Microcosms were constructed from 50 mL Falcon tubes (30 mm dia x 110 mm height) and included 20 mL of sediment. The microcosms were contained within two water baths inside an incubation chamber which regulated the environment within the microcosms and allowed waterflow between microcosms (Fig S1). We grew midges and algae over 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). On days 14 and 22 of the experiment, we measured primary production by capping the microcosms and measuring the production of dissolved oxygen. We then destructively sampled the midges within a subset of microcosms to determine the effects of the initial algal abundance on midge survival and growth.

On August 4th, 2020, we collected both midge larvae and sediment from a single location in Mývatn’s southern basin using a Kajak corer on a single day. Using a 125 μm sieve, we extracted midges from the sediment and selected live Tanytarsini individuals that were roughly the same size. Following a 24h gut clearance period in tap water, twenty individual midges (~28,000 ind m-2) were added to half of the microcosms. This density is well within the range for Mývatn where larval midge densities range between 0 and 500,000 m-2 (Thorbergsdóttir et al. 2004). This density is therefore unlikely artificially alter the observed midge growth rates or consumption rates (Hillebrand 2009).

We added 20 mL of sediment to each microcosm in two layers. The top 2 mL contained our manipulated sediment, containing a range of algal abundance. We combined sieved surface sediment (taken from the top 0-0.75 cm of kajak cores) with sieved bottom sediment (taken from 5-10 cm below the surface) along a serial dilution. Thus, the fraction of surface sediment in the top 2 mL of microcosms ranged from 1, 1/2, 1/4, 1/8, 1/16, 1/32, 1/64, 1/128, 1/256, and 0. The bottom 18 mL of the microcosms contained unsieved bottom sediment (5-10 cm below the surface). We sieved both the surface and bottom sediment used for our sediment treatment through 125 μm to remove midges from the surface layer and to aid in homogenizing the sediment. The bottom 18 mL was left intact to retain high interstitial nutrient concentrations (Gíslason et al. 2004) to support algal growth.

To evaluate the efficacy of our sediment manipulations in generating a range of algal concentrations, we measured chlorophyll-a and organic content. To obtain chlorophyll-a content, we froze 1 mL of sediment for >24h and extracted chlorophyll in methanol for 24h. We measured chlorophyll by fluorescence (AquaFluor, Turner Designs, San Jose, CA, USA) before and after acidification (120 μL of 0.1N HCl) (Holm-Hansen and Riemann 1978). We measured organic content by measuring the change in mass between sediment following drying (60C for >24h) and combustion (550C for 5h). These measurements suggest that we generated a range of live algal concentration (Fig. S2). However, consistent with Poulíčková et al. (2008) (Poulíčková et al. 2008) low algal concentrations were detectable even in the microcosms with no surface sediment (Fig. S2).

The microcosms were kept in an incubation chamber at ~12 °C under actinic lights (TrueLumen Pro, Current USA, Vista, CA, USA), which produce 1,000 lumens m-2 of blue light. This setup has been previously shown to allow for high productivity of epipelic algae from Mývatn (Ives, unpublished analysis). We assume this light level to be past the point of light saturation based on preliminary observations (i.e., additional light should not increase production) and there is no evidence of photoinhibition in epipelic algae at Mývatn (McCormick et al. 2021). The lights were set at 18:6h day:night to match the natural photoperiod. Air temperature and light were monitored with a HOBO logger (Onset Computer Corporation, Bourne MA, USA) (Fig. S3).

72h after adding midges to their microcosms (ample time for midges to build tubes), we submerged the microcosms in one of two common water baths within the incubation chamber. Each water bath contained air stones to ensure microcosms with low algal concentrations did not become anoxic. Although *Tanytarsus sp.* are thought not to abandon tubes readily, we added mesh tops to the microcosms which extended out of the water (Fig S1) to reduce the chance that midges dispersed. This ultimately proved ineffective (see below).

## 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 gross primary productivity (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 via 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, Yellow Springs, Ohio, USA). During the incubations, we sealed the microcosms with airtight screw on 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 ~11 h to ensure a detectable signal of NEP and ER across all algal concentration treatments while avoiding supersaturation and anoxia.

## Midge Survival and Growth

Immediately following the 24h gut clearance period and both incubations, we destructively sampled a subset of the microcosms to measure midge size. We measured three replicates after the gut clearance period. After the first incubation date, we destructively sampled 2 replicates from each treatment and sampled the remaining 3 replicates after the second incubation date. For simplicity, we refer to sampling event for both the incubation and the midge samples as these days (day 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 the instar and measured their 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 (Fig S4).

For each microcosm that was stocked with midges, we estimated the growth rate of midges, expressed as the change in ash free dry mass (AFDM) per day. Because we did not mark individual midges and measure them twice, we could not calculate growth rates for each individual. Therefore, we estimated the mean and uncertainty in individual growth rates for each treatment using non-parametric bootstrapping. 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). Then, we calculated the mean individual mass in each treatment resampled 1,000 with replacement times using the “sample\_n” function in the dplyr package (v. 1.0.6; Wickham et al. 2021) in R (R Core Team 2021). Lastly, we used the bootstraps to calculate the mean and standard error of the average daily growth rates between the initiation of the experiment and each sampling event for each treatment.

## Data Analysis

To assess the effect that midges had on primary production (GPP), we used linear models (LMs). We included a term for initial algal abundance as a continuous predictor ranging from 0 (no surface sediment) to 1 (ambient densities of algae, 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 a term for the water bath that the microcosms were in as a fixed effect. Rather than fit a single model with a three-way interaction (incubation date x midge treatment x initial algal abundance), we fit the days separately to aid in interpretation and because variance differed between incubation days.

To examine the effect that initial algal abundance has on midge survival and growth, we fit linear models on two different response variables: the number of midges in a microcosm and midge body length. We used a quasi-Poisson generalized linear model (GLM) on the number of midges in a microcosm. This model included fixed effect terms 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 midges collected. The fixed effects for this model were the same as described above. However, it differed in that it included a microcosm level random effect, as there were multiple measurements (i.e., midges) per microcosm. As with GPP, all models were fit separately to the two sampling events.

Lastly, we compared primary production and midge growth. We converted midge growth and primary production to comparable units. Primary production values were converted from oxygen production to carbon production (μg C cm-2d-1), assuming a photosynthetic quotient of 1 (Thorbergsdóttir and Gíslason 2004, McCormick et al. 2021). We also converted average somatic midge growth from AFDM into μg C ind-1d-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 version 4.1.2, (R Core Team 2021). We fit LMs using the “lm” function in the “stats” package, GLMs using the function “glm” in the “stats” package, and linear mixed effects models using “lmer” in the “lme4” package (v.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 (v. 3.0-12; Fox and Weisberg 2019). For all models, we also dropped all interactions to assess the significance of the main effects with Type II tests. The measurement error model was fit using the “pgls.Ives” function in the phytools package (v. 1.0-1; Revell 2012).

## Model

The experiment gives an empirical relationship between the contemporaneous resource supply and the somatic growth of midges over the course of the experiment. This relationship is determined by the per capita growth rates of algae and the consumption rates of midges, two factors that could not be manipulated experimentally in the microcosms. Nonetheless, understanding the effects of per capita algal growth rates and midge consumption rates on patterns of resource supply and consumer growth could give insight into interactions between consumers and their rapidly growing resources. Therefore, we fit a model of algal and midge growth to our experimental data, which then allowed us to investigate the expected consumer-resource dynamics under different algal growth and midge consumption rates.

We chose a simple model to relate resource and consumer growth to fit to our experimental data, because a more biologically realistic model would have been statistically intractable given the available data. The model, iterated over a daily timestep, is:

Here, is resource biomass. Because we could not collect both midges and sediment from the same microcosms, we do not have direct measures of algal biomass. Instead, we let be the photosynthetic potential of algae, that is, the rate of photosynthesis of the algae under saturating light conditions, like those we believe that we achieved with the actinic lights. Because GPP is driven by both 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 measured the mass of each midge in the experiment, so we let be the average mass of an individual midge on day t.

In the model, the rate that the photosynthetic potential of algae increases is determined by its maximum per capita growth rate, , and density-dependent effects (e.g., self-shading and nutrient limitation), *b*. When *b* < 1, per capita algal growth diminishes with increasing . Algal photosynthetic potential is consumed by midges with a consumption rate *a*, and the efficiency with which it is converted into midge biomass is scaled by . is equivalent to the midge gross production efficiency, which is the fraction of biomass consumed that is not egested, excreted, and respired (Benke and Huryn 2017). In the model, the consumption rate of midges depends upon their biomass so that larger midges have a higher consumption rate (e.g., to support higher metabolic costs).

We fit the model to data from the microcosm experiment. The only available measure of algal photosynthetic potential () at the inception of the experiment was chlorophyll-a concentration, which is highly correlated with GPP under light saturating conditions (e.g., McCormick et al. 2021). was fit to data that was standardized by dividing by the mean. Because we had two different measurements (chlorophyll-a and GPP), they were standardized separately, and we included a fitted parameter that converts between scaled chlorophyll-a concentrations and scaled GPP. was fit to average individual mass of midges in each microcosm standardized by the grand mean across all treatments and sampling days. Therefore, both and are dimensionless. Under the assumption that the variance of the residuals scaled with the log of and (as supported by examination of the data), we fit the model by minimizing the sums of squared residuals between log observed and log predicted values using the “optim” function in the native “stats” package in R.

Simulating the fitted model allowed us 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 starting midge biomass as used in the experiment and then simulated and for 22 days, the duration of the experiment. We report values of light saturated GPP on a given day, , average midge mass,, and average daily midge growth rates, , converted back to original units.

# Results

## Experiment

On day 14, GPP was positively related with initial algal abundance, unrelated to the presence of midges, with the initial algal abundance x midge interactions being nonsignificant (Fig 1A, Table 1). In contrast, there was a significant initial algal abundance x midge interaction on day 22, with the positive association between GPP and initial algal abundance only maintained in the presence of midges. When midges were absent, GPP in the microcosms with the lowest initial algal abundance increased to reach the same level as ambient initial algal abundance. Together, these results imply that initial differences in algal biomass could be compensated for by growth, but only in the absence of consumption by midges. There was a difference in the GPP between the two water baths on day 22, which may be due to variation in the environment experienced by the two water baths within the incubation chamber (Fig S3).

Midges were more abundant and larger in microcosms that had higher initial algal abundance. We found more live individuals in microcosms with higher resource availability on both days 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. 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 level of movement of individuals between the microcosms. On both days 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 resource availability (Fig 1C; Table 3). Similar patterns were seen for midge development rates (the proportion of individuals that progressed past 2nd instar; Fig S5, table S1).

Estimated average individual midge growth rates were positively associated with the algal primary production rates on the two incubation days (Fig 2). For some microcosms with low initial algal biomass, average growth was negative, which could be the result of reductions in size due to starvation or disproportionate mortality among the larger individuals in resource limited microcosms. Midge growth appear to have slowed in the microcosms with ambient algal abundance on day 22, as evidenced by lower growth between the average midge on day 22 than in day 14 (Fig 2).

## Model

Using our dynamic consumer-resource model, we assessed how changes in the consumption rate might influence the relationship between primary production and midge growth that we observed in the experiment. We fit the model to the data (Fig. S6), which yielded the parameters in table 4. Next, we varied the consumption rate (a) and plotted the resulting daily midge growth rate at t=22 (matching our experiment) for each initial algal biomass used in the experiment (Fig. 3). As expected, midge growth rate had a hump-shaped relationship with the consumption rate. Intuitively, over short timescales, higher initial resource availability increased consumer growth at the optimum consumption rate. The consumption rate estimated from the observed data was below the optimum on day 22. Therefore, the model implies that midges could have maximized their short-term growth over the course of the experiment with a higher consumption rate. These differences between initial algal abundance are transient because the saturation point of midge size does not differ between different starting values. The optimum attack rate differs between days (as illustrated for day 14 in Fig S7). Generally, the longer consumers and resources interact and midges accumulate biomass, the optimum decreases, because it allows consumers to accumulate biomass for longer before their biomass becomes so large that that the resource biomass is unable to support further growth.

Altering consumption rate and maximum per capita resource growth rate resulted in different patterns of midge growth and primary production on day 22 than we observed in the experiment (Fig 4A). These generated qualitatively similar relationships between midge growth and primary production, but the magnitude of midge growth and primary production differ. When the attack rate is below the optimum or when resource growth rates are reduced, high midge growth rates are associated with comparatively higher rates of primary production. When the consumption rate is increased above the optimum or the resource growth rate is increased, high midge growth rates are associated with lower relative primary production rates. Above the optimum consumption rate, both projected midge growth rates and primary production are reduced relative to the optimum, but increased resource growth rates always increased both midge growth and primary production.

A comparison of the dynamics underlying these patterns explain this switch (Fig 4B). Despite very different dynamics, the mechanism underpinning this pattern is the same: the accumulation of midge biomass. When algal photosynthetic potential (our measure of algal biomass, ) and midge biomass () increase, so does the rate at which midges remove algae (). When the attack rate (a) is increased, midges more rapidly reduce , but the biomass that midges have already accumulated remains in the system. Higher initial algal abundance means this happens sooner. Similarly, when the per capita algal growth rate is increased, the rate of midge biomass accumulation () increases, but eventually the accumulated midge biomass becomes so high that algal growth can no longer support continued consumption and decreases. Again, when initial algal abundance is higher this happens sooner.

# Discussion

In this study, we explored the feedbacks between a consumer (the midge *T. gracilentus*) and its continuously growing resources (epipelic algae). First, we performed a microcosm experiment, where we manipulated the initial abundance of algae (via sediment dilutions) and presence of midges at a low density. We found that midge consumption exerted top-down control on primary production. We also found 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 on both sampling events. Using a model parameterized by the experiment, we then explored how the consumption rate and algal growth rates influence patterns of primary production and midge growth.

Our experimental results show that *T. gracilentus* somatic growth depends on contemporaneous resource supply. 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 resource growth rates via shading results in lower midge survival, growth, and emergence (Wetzel et al. 2021, Phillips et al. 2021b). Studies on other midge species that have reduced food quantity directly 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). One study on snails (Cross and Benke 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 suppressed the growth of the epipelic algae under high light conditions. This result is consistent with studies on invertebrate grazers in streams which illustrate that grazers can slow the development of standing 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).

The reciprocal interactions between midges and algae generated a positive relationship between primary production and midge growth during the experiment. However, our model illustrates that consumer growth is not necessarily positively related to the biomass of their resources at a given time, despite the cumulative resource supply driving consumer growth. This occurs because midge biomass is accumulated over time while the turnover of algae can be relatively rapid. Increases to midge biomass, either through increases in consumption rates or increases in the growth rate of algae (Similar to the paradox of enrichment; Rosenzweig 1971), resulted in overexploitation. This positive relationship between longer-lived consumer biomass and instantaneous rates of primary production (or the biomass at any given time of a shorter lived resource species) only occurs when resource growth rates exceed the removal rate by consumers. Our estimated parameters suggest, therefore, that the relatively low density of midges did not overexploit their resources during this experiment.

Our finding that midges did not overexploit algae may partly help to explain how midges are able to undergo such 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 longer lived primary consumers often have traits that boost the rates at which their resources grow. *T. gracilentus* build silk tubes which appears to increase algal growth rates by alleviating light limitation (Phillips et al. 2019), which can increase the number of midges able to emerge (Phillips et al. 2021a). This positive effect of silk structures on algal production has been found on other tube building aquatic herbivores (Pringle 1985, Ings et al. 2010, Tumolo et al. 2019). Bioturbating 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 the nutrients available or the rate of nutrient cycling which can support higher resource growth rates (André et al. 2003, Ings et al. 2012, Mooney et al. 2014, Hölker et al. 2015). Thus, many longer lived consumers may modify the environment experienced by resources in ways that improve their resource supply and enhance their own growth.

While midges did not overexploit their resources in our experiment, whether the balance between consumption and resource growth observed in this experiment translate to dynamics in the lake is uncertain. Environmental factors underpinning ecological rates vary substantially over space and time. For example, algal growth rates are often determined by nutrient concentrations (Schindler 1974), light availability (Jassby and Platt 1976, Cantonati and Lowe 2014), and temperature (Raven and Geider 1988, Brown et al. 2004). Temperature also influences ectotherm consumption rates (Savage et al. 2004, Gilbert et al. 2014, West and Post 2016, Synodinos et al. 2021). At Mývatn, thick cyanobacteria blooms can slow or even halt epipelic algal growth rates (Vadeboncoeur et al. 2008, McCormick et al. 2021). Pelagic nutrient concentrations vary spatially (Dickman et al. 1993) and temporally (Einarsson et al. 2004). Air temperatures vary seasonally, show evidence of a warming trend between 1979 and 2000 (Björnsson and Jónsson 2004), and the springs that flow into Mývatn differ in temperature (Einarsson et al. 2004). This variation likely results in spatiotemporal variation in the optimum consumption rate. If midge consumption is unable to adapt to this variation, it would result in spatiotemporal variation in the balance between consumption and algal growth. However, midges may not be entirely at the whim of environmental variation.

Although our experiment was not designed to study midge movement, we found evidence that *T. gracilentus* moved between microcosms and our experiment provides some insight into this behavior. Our findings that midges moved run contrary to the observations by Chaloner and Wotton (1996), who suggested that lotic *Tanytarsus sp.* are stationary once building tubes due to the high cost of building such robust tubes. No other study to our knowledge has documented movement by late instar *Tanytarsus* sp, but movement by larval tube-building chironomids is generally understudied. The microcosms which had more midges than we stocked with all had high initial algal concentrations and on both sampling events, midges were found in microcosms that were not stocked with midges tracked patterns of productivity. Midges found in microcosms that were not stocked with midges also tended to be smaller, consistent with the hypothesis that resource limited midges moved more frequently (Wiley and Warren 1992). Movement of smaller midges may also be unrelated to resource because there may be ontogenetic shifts in movement. Data across other species of midges suggest that movement by midges may be less frequent in later stage larvae in other stages (Davies 1976, Baker and Ball 1995). If our resource limitation hypothesis is correct, these observations are consistent with theory and empirical evidence suggesting that consumers ought to move when the cost of acquiring resources exceeds the energy gained from those resources (Pyke 1984, Morris 2006, Mueller and Fagan 2008, Abrahms et al. 2020). If the latter hypothesis is correct, resource limitation would still increase movement rates, but only by slowing development rates.

Many consumers feeding on contemporaneously growing resources move in response to resource supply which may contribute to the spatial structure of their resources. For example, algivorous catfish aggregate in unshaded areas where algal growth rates are high (Power 1984). This increased grazing pressure in unshaded areas contributes to equivalent standing algal biomass between shaded and unshaded stream reaches (Power 1984). Similarly, benthic macroinvertebrate drift is often thought to be associated with resource limitation. For example, rates of drift were found to be much higher in streams with more nutrient limited algae (Hershey et al. 1993). Other tube-building midges have been observed abandoning their tubes and settling in new areas after overgrazing the algal community (Wiley and Warren 1992, De Haas et al. 2006). Given the increase in GPP in microcosms that were not stocked with midges, this abandonment may allow for recovery of their resource supply within a generation. Habitat abandonment and resettlement, therefore, may serve as a strategy for consumers to maintain unsustainable harvesting levels or weather environmental variation. As a consequence, mobile consumers feeding above sustainable levels can contribute to a dynamic spatial structure of their resources (van de Koppel et al. 2005, Betini et al. 2017).

# Conclusions

Consumers with much longer generation times than their resources must balance the growth of their resources and consumption. Our model suggests that a negative relationship between the biomass of longer-lived consumers and instantaneous measures of their resource biomass is evidence of overconsumption. In an experiment with *T. gracilentus,* we found evidence that midges appeared to manage their resources well. While it is unclear whether midges or other consumers can optimize their consumption rates in response to spatiotemporal variation in their resource supply, consumers often employ behaviors that may 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 movement in response to spatial structure in resource supply. How consumers manage their resources in a dynamic environment may shape their somatic growth rates and subsequently their population dynamics.

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# Author contributions

JCB and ARI conceived of the study. JCB designed the experimental methods. JCB, ARI, and KRB conducted field and laboratory work. JCB performed analyses with feedback from ARI, JSP, and KRB. JCB wrote the first draft of the manuscript and all coauthors contributed substantively to subsequent drafts and provided final approval.

# Data and Code Availability

All data and code used in this manuscript are available on Zenodo (**LINK**).

# Tables

Table 1: Effects of our sediment and midge treatment on GPP on the two incubation days with and without interactions (type III and type II tests, respectively). Models were fit with and without interactions. P values were calculated on the basis of their t statistic. Initial algal abundance is the proportion of surface sediment 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 Stocked | -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 x Midges Stocked | 0.164 | 0.334 | 0.739 |  |  |
| Day 22 |  |  |  |  |  |
| Initial Algal Abundance | -1.07 | -1.482 | 0.144 | 0.809 | 0.422 |
| Midges Stocked | -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 x Midges Stocked | 2.994 | 2.921 | 0.005 |  |  |

Table 2: Effects of our sediment and midge treatments on the number of midges present in a microcosm. Data were analyzed using a quasipoisson GLM fit to days separately. Models were fit with and without interactions (type III and type II tests, respectively). P values were calculated on the basis of the T statistic. Initial algal abundance is the proportion of surface sediment 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 Stocked | 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 x Midges Stocked | -0.422 | -2.538 | 0.016 |  |  |
| Day 22 |  |  |  |  |  |
| Initial Algal Abundance | 0.124 | 1.636 | 0.108 | 3.862 | 0.0003 |
| Midges Stocked | 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 x Midges Stocked | -0.032 | -0.402 | 0.689 |  |  |

Table 3: Effects of our sediment and midge treatments on the body length of midges in mm. Data were analyzed using a linear mixed effects model with microcosm id as a random effect. Models fit to days separately and were fit with and without interactions. 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 is the proportion of surface sediment and was log transformed.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  |  | Type III | | Type II | |
|  | Estimate | Fndf,ddf | P | Fndf,ddf | P |
| Day 14 |  |  |  |  |  |
| Initial Algal Abundance | 0.028 | 0.1631,213.492 | 0.686 | 33.6401,12.511 | <0.0001 |
| Midges Stocked | 0.426 | 6.9541,52.169 | 0.011 | 7.1001,66.701 | 0.0097 |
| Water Bath | -0.048 | 0.4861,13.051 | 0.498 | 0.6461,13.636 | 0.435 |
| Initial Algal Abundance x Midges Stocked | 0.071 | 0.9861,174.214 | 0.322 |  |  |
| Day 22 |  |  |  |  |  |
| Initial Algal Abundance | 0.104 | 5.3101,134.365 | 0.023 | 15.0211,41.093 | 0.0004 |
| Midges Stocked | 0.124 | 0.4781,71.494 | 0.592 | 3.7431,88.798 | 0.056 |
| Water Bath | 0.033 | 0.1361,41.983 | 0.715 | 0.0801,42.552 | 0.779 |
| Initial Algal Abundance x Midges Stocked | -0.024 | 0.2131,84.949 | 0.645 |  |  |

Table 4: Parameters of the consumer-resource model (Eq. 1) estimated from the experimental data. Parameters as in Eq. 1.

|  |  |  |
| --- | --- | --- |
| Parameter | Definition | Estimated value |
| 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 | 0.21 |

# Figure Legends

Figure 1: A, GPP increased with initial algal abundances. On day 22, GPP no longer was related to initial algal abundance in the absence of midges. B, we found higher numbers of live midges 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 number of midges (B) and average initial body length (C). Note the x axis for all figures are on a log scale.

Figure 2: Primary production and the average growth rate of midges in the laboratory experiment were positively related. Variation in primary production was driven by changes in intial algal abundance. Vertical and horizontal bars show 1 standard error. The line shows the fit of the measurement error model. The measurement error model predicted a slope of 18.96 and an intercept of 3.15. Microcosms had an area of 7.1 cm2 and had 11.6 midges on average, but densities differed between treatments.

Figure 3: There is a consumption rate that maximizes projected midge growth over the experimental duration. The x axis shows the consumption rate of midges on algae (a), and the y axis shows the projected daily midge growth. Lines are colored by initial algal abundance, which generated variation in Xt at day 0. The vertical line shows the consumption rate estimated from our data. All parameters used in the fitting are in table 4.

Figure 4: A, Projected patterns of average daily midge growth ((Yt - Yt=0)/t) and primary production (Xt) under different resource growth rates and initial resource availability (set to those values used in the experiment) on day 22 (t=14 in Fig S8). Initial consumer biomass (Yt=0)for all treatments was equal. Lines connect points across initial resource biomasses. B, Dynamics of projected midge (dashed) and GPP (solid) over the attack rates and resource growth rates used in 4A. Only the highest and lowest initial algal abundances are shown to aid in visualization and line colors match point colors in 4A. Unless stated, all parameters are as in table 4.

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