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Spatiotemporal variation in the sign and magnitude of ecosystem engineer effects on lake ecosystem production

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Abstract. Ecosystem engineers can have diverse and conflicting effects on their ecosystems, and the balance between these effects can depend on the physical environment. This context dependence means that environmental variation can produce large differences in engineer effects through space and time. Here, we explore how local variability in environmental conditions can lead to large spatiotemporal variation in the effect of tube-building midges on benthic ecosystem metabolism in a shallow subarctic lake. Using field experiments, we found that midge engineering increases both gross primary production (GPP) and respiration (RESP) in the sediment. Gross primary production and RESP have opposing influences on net ecosystem production, and the net effect of midges on the benthic ecosystem depends on the balance between their effects on GPP and RESP. Variation in light mediates this balance—under high light conditions, primary producers are able to exploit the structural benefits provided by midges, while in the dark, the elevation of respiration from midge engineering predominates. Benthic light levels vary spatially and temporally due to episodic cyanobacterial blooms that prevent almost all light from reaching the benthos. By quantifying the nonlinear relationship between midge engineering and light, we were able to project ecosystem-wide consequences of natural variation in light conditions across the lake. Our results illustrate how the sign and magnitude of ecosystem-wide effects of ecosystem engineers can vary through space and time.

Key words: *Chironomus islandicus;* context dependence; lake metabolism; light limitation; macroinvertebrates; nutrient limitation; *Tanytarsus gracilientus*.

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Introduction

Ecologists have long been interested in the potential for single populations to have disproportionate influences on their ecosystems (Paine 1966). Striking examples come from ecosystem engineering, whereby a single species alters the physical environment experienced by many others, with cascading consequences for the whole system (Jones et al. 1994, Bertness and Leonard 1997, Wright and Jones 2006). Different organisms in a community respond to environmental changes in different ways, leading to multiple effects of ecosystem engineering at the community and ecosystem scale (Jones et al. 1997, Hastings et al. 2007, Gribben et al. 2013). Ecosystem engineers also have non-engineering effects on other organisms within a community

through direct interactions such as competition and herbivory (Jones et al. 1997, Bertness et al. 1999, Hastings et al. 2007, Largaespada et al. 2012). The net impact of ecosystem engineers depends on the balance between these diverse and potentially conflicting effects, which itself can depend on the environmental context (Bertness et al. 1999, Norkko et al. 2006, Daleo and Iribarne 2009, Brown and Lawson 2010, Lathlean and McQuaid 2017).

The context dependence of ecosystem engineering means that environmental variation can produce large differences in engineer effects through space and time (Wright et al. 2006, Hastings et al. 2007). For example, many engineers provide refuges from stressful environments (e.g., temperature or physical disturbance), and the response of other organisms in the communities varies across gradients in stress (e.g., tidal height or latitude; Bertness et al. 1999, Crain and Bertness 2005, Arribas et al. 2014). While previous studies have demonstrated the existence of variation in the effects of ecosystem engineering across a range of scales (Wright et al. 2006, McAfee et al. 2016, Lathlean and McQuaid 2017), few studies have attempted to predict the magnitude of spatiotemporal variation in engineering effects at the ecosystem scale. Scaling small-scale engineering to ecosystem-wide effects requires (1) modeling the functional response of engineering to continuous variation in the environment and (2) quantifying the spatial and temporal variation in the environment within the region of interest (Wright et al. 2006, Hastings et al. 2007). This is particularly important because responses of engineering to environmental conditions are likely nonlinear (as is true for many ecological processes) and the shape of this nonlinearity could have large consequences for the overall effects of engineering in variable environments (Ruel et al. 1999).

Here, we explore how local variability in environmental conditions can lead to large spatiotemporal variation in the effect of tube-building midges on benthic ecosystem metabolism in Lake Mývatn, Iceland. Midges (Diptera: Chironomidae) are widespread in lakes worldwide and exemplify other benthic invertebrates (e.g., annelids and mollusks) in their roles as ecosystem engineers (Armitage et al. 1995, Gutiérrez et al. 2003, Norkko et al. 2006, Arribas et al. 2014, Hölker et al. 2015). Larval midges construct silk tubes and a network of silk that stabilizes and provides three-dimensional structure to the sediment (Olafsson and Paterson 2004, Hölker et al. 2015; Fig. 1). In Mývatn, midge populations are highly variable but can exceed densities of 200,000 m^{-2} and compose a majority of animal biomass in peak years (Lindegaard and Jónasson 1979, Einarsson et al. 2004). Therefore, Mývatn's midges have the potential to greatly alter benthic ecosystem function (Fig. 2). We examined midge effects on net ecosystem production (NEP), which equals gross primary production (GPP) minus respiration (RESP; Lovett et al. 2006, Chapin et al. 2006). Net ecosystem production is a central component of ecosystem carbon budgets that influences the biomass available across trophic levels and the exchange of dissolved CO_2 with the atmosphere (Randerson et al. 2002, Cebrian and Lartigue 2004, Chapin et al. 2006, Davidson et al. 2015). There is much current interest in the biotic and abiotic factors determining the balance between GPP and

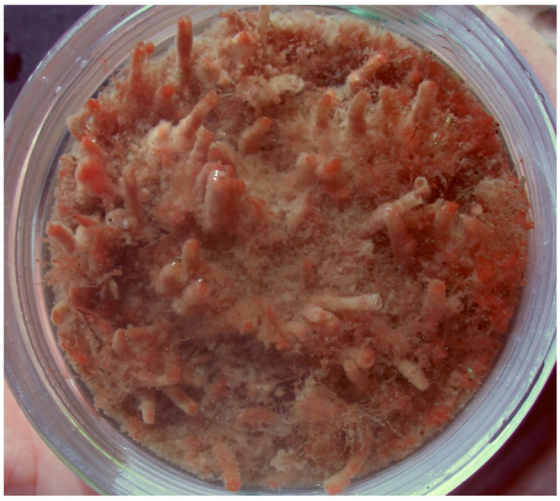

Fig. 1. Midges build silk tubes that provide a substrate for algal growth. The sediment core in the photograph was taken from the bottom of Mývatn using a Kajak corer in a year of moderate midge abundance. The cylindrical structures projecting from the sediment surface are the silk tubes constructed by the midge larvae. Diatoms grow on the tubes and in the sediment. The image is in false color, replacing infrared with red to highlight the distribution of chlorophyll, which is more concentrated on the midge tubes than in the surrounding sediment. Photo credit: T. Ives.

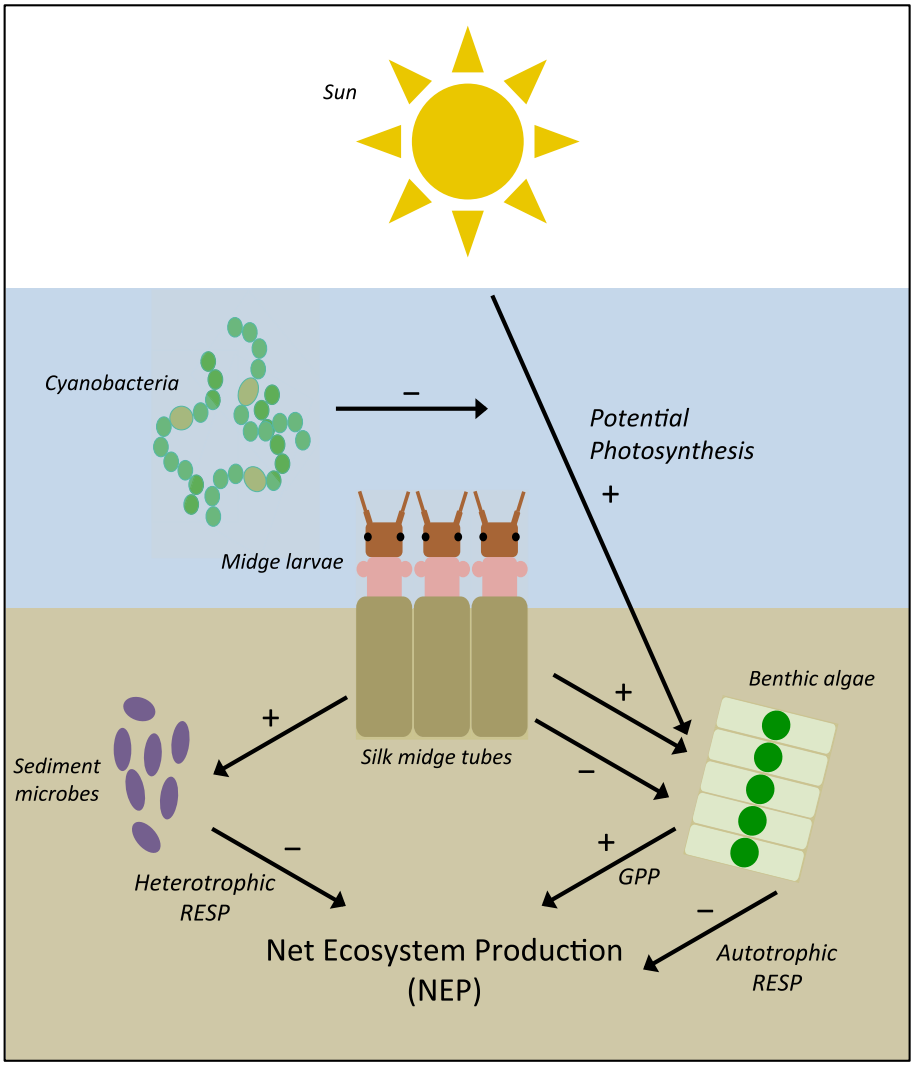

Fig. 2. Midges can alter benthic ecosystem function. Larval midges build silk tubes that provide a substrate for algal growth and increase gross primary production (GPP) in the sediment. However, midges may inhibit GPP through consumption of algae. Furthermore, midges can stimulate microbial respiration (RESP) by oxygenating the sediment. Gross primary production and RESP have opposite effects on net ecosystem production (NEP), so the effect of midges on NEP depends on the balance between their effects on GPP and RESP. We hypothesized that light mediates this balance, because the positive effects of midges on GPP would decline as photosynthesis became more limited by light. Episodic cyanobacterial blooms have a negative effect on benthic light levels, which could result in spatiotemporal variation in the net effects of midges on benthic production.

RESP in both aquatic and terrestrial systems, particularly in the context of global environmental change (Belshe et al. 2013, Demars et al. 2016, Holgerson and Raymond 2016).

Previous work showed that midges can increase GPP and producer biomass, possibly by providing a substrate for algal growth; chlorophyll concentrations can be twice as high in the tubes compared to the surrounding sediment (Pringle 1985, Olafsson and Paterson 2004, Hölker et al. 2015, Herren et al. 2017). However, midges may also decrease GPP through direct consumption of primary producers. Midges may ameliorate short-term nutrient limitation of GPP

through mobilization (e.g., excretion or bioturbation) of N and P, but can also reduce P availability by oxidizing the sediment (Henriksen et al. 1983, Svensson 1997, Zhang et al. 2010, Hölker et al. 2015, Benelli et al. 2018). Furthermore, sediment oxygenation can increase microbial RESP by changing redox conditions and inducing shifts in bacterial community composition (Svensson and Leonardson 1996, Yeager et al. 2001, Nogaro et al. 2008, Hölker et al. 2015, Baranov et al. 2016*a*, *b*). Therefore, midges may have opposing effects on NEP through their various effects on GPP and RESP (Fig. 2). Determining how the physical environment regulates the balance of midge effects on production and respiration is important for understanding their role in the functioning of lake ecosystems (Hölker et al. 2015).

With two field experiments, we (1) explored the mechanisms by which midges stimulate benthic GPP and RESP and (2) quantified the role of light in mediating the balance between these effects and the consequences for NEP. In the first experiment, we experimentally mimicked two ways in which midges alter the benthic environment: modification of sediment structure and nutrient mobilization. We predicted that if midges stimulate ecosystem metabolism through these mechanisms, then experimental manipulations should (1) approximate the effects of midges when midges are absent and (2) be at least partially redundant with midges such that they have weaker effects when midges are present. We were interested in comparing the effects of midges through sediment structure and nutrient mobilization, because structural effects would be largely predictable from the presence of midges (Hölker et al. 2015). In contrast, effects of nutrient mobilization would depend on the ambient nutrient content in the sediment pore water, which is highly dynamic in Mývatn (Gíslason et al. 2004).

In the second experiment, we quantified NEP across a light gradient in the presence and absence of midges. We expected the positive effect of midges on GPP to decline as photosynthesis became more limited by light, as the potential benefits provided by midges could only be exploited by the primary producers in the presence of sufficient light for photosynthesis. In contrast, we expected the positive effects of midge on RESP (at least from heterotrophs) to be present in both light and dark conditions. Therefore, a decline in light would tip the balance between positive midge effects on GPP and RESP, making the midge effect on NEP less positive or more negative (Fig. 2). In Mývatn, benthic light levels vary spatially and temporally due to variation in depth and episodic cyanobacterial blooms that prevent almost all light from reaching the benthos (Einarsson et al. 2004). To investigate how this spatiotemporal variation in light intensity can alter midge effects on NEP, we combined data on patterns of light transmission throughout the lake with a model parameterized from our field experiments. This allowed us to project the potential consequences of spatiotemporal variation in environmental conditions for determining the effect of midge engineering on NEP at the whole-lake scale.

Methods

Study system

Mývatn is located in northeastern Iceland (65°40′ N, 17°00′ W) and has a tundra–subarctic climate (Björnsson and Jónsson 2004). The lake is shallow (mean depth ≈ 2.5 m and max depth ≈ 4 m in main basin) and is fed by cold and warm springs rich in phosphorus (N, P, and Si loading of 1.5, 1.4, and 340 $g \cdot m^{-2} \cdot yr^{-1}$, respectively; Ólafsson 1979, Einarsson et al. 2004). Most of the primary production (roughly 288 g $C \cdot m^{-2} \cdot yr^{-1}$) is benthic (Einarsson et al. 2004) as is likely true for many shallow lakes (Vadeboncoeur et al. 2002, Karlsson et al. 2009). Diatoms are the dominant benthic producers, with the genus *Fragilaria* composing most of the algal biomass (Jónasson 1979, Einarsson et al. 2004). Benthic primary production supports large populations of midges (>30 species), and the dominant tube-building genera *Tanytarsus* (tribe Tanytarsini) and *Chironomus* (tribe Chironomini) compose a majority of the lake's animal biomass in peak years. *Tanytarsus* generally has two generations per year accompanied by large emergences of adults that greatly reduce the number of larvae in the sediment. Furthermore, many of Mývatn's tube-building midge show large interannual fluctuations in abundance, with *Tanytarsus* spanning several orders of magnitude between high- and low-midge years (Ives et al.

2008). It is unknown how long the midge tubes persist following emergence, but they probably degrade within a few weeks.

Experimental methods

Mesocosms.—We performed two field experiments to explore (1) the mechanisms of positive midge effects and (2) light mediation of midge effects on benthic ecosystem metabolism. The experiments used mesocosms constructed from acrylic tubes (33 cm height × 5 cm diameter) with the bottom 15 cm filled with sediment and the top 18 cm with lake water. In both experiments, we manipulated the presence/absence of midges and their associated engineering to quantify their effects on ecosystem metabolism. A previous experiment at Mývatn directly demonstrated positive effects of midges on GPP and NEP by adding different midge densities to sediment that was sieved to remove any naturally occurring midges (Herren et al. 2017). In contrast, our goal was to quantify the magnitude of midge effects under the most realistic conditions possible, so we could place midge engineering in the context of natural environmental variability. Adding midges to sieved sediment does not accomplish this, because it takes time for the midges to recover from being relocated and for the impact of midge tube building to be fully realized in the sediment structure. Instead, we filled the mesocosms with either intact sediment cores (midge present) or sediment sieved to remove midges and disrupt the structure created by midge tubes and silk (midge absent). Mývatn's sediment is composed of very fine particles (primarily diatom frustules and volcanic tephra; Einarsson et al. 2004), and in the natural absence of midges, the sediment has a very loose structure that was closely mimicked by the sieved sediment (Olafsson and Paterson 2004). Therefore, our midge treatments reflected the natural contrast in sediment structure between years of high- and low-midge abundance.

For the midge-present treatments, we extruded the top 15 cm of sediment cores containing larval midges into each mesocosm without disturbing the sediment. For the midge-absent treatments, we sieved the top 5 cm (containing most of the active algal cells) and bottom 10 cm of sediment cores through 63-μm and 125-μm mesh, respectively, pooled the two sediment layers from all cores, and reassembled them as two layers in the mesocosms. The use of 63-μm mesh for the top layer was necessary to remove first-instar larvae that typically reside near the sediment surface. Sieved sediment was stored in a cool dark location for 2–3 d prior to establishing the mesocosms so that the sediment could settle, while cores for midge-present treatment were collected on the day each experiment was deployed. The sediment cores were collected from Mývatn using a Kajak corer, at times and locations of moderate larval midge density (15,000–25,000 m^{-2}). For both midge-present and midge-absent treatments, the bottoms of the mesocosms were sealed with foam stoppers and tape. The bottom 15 cm of each mesocosm was wrapped with four layers of black plastic to replicate the naturally dark conditions within the lake sediment.

Sieving and storing of sediment was clearly a large perturbation that could have altered algal abundance, productivity, or microbial activity. However, chlorophyll-a concentrations were similar between sieved and intact sediments (Appendix S1). Furthermore, there were no indications of transient shifts in ecosystem metabolism of the sieved treatments that were not also present in the intact treatments; the sieved treatments were actually more consistent through time (*Results*; Appendix S1). While this does not demonstrate that sieving had no artificial effects, it does suggest that the sieved treatments quickly reached an equilibrium state with their surrounding environment (consistent with the fast turnover times of diatoms that are the dominant benthic producers; McCormick and Stevenson 1991, Sommer 1991) and provide a consistent baseline for evaluating the effects of midge engineering.

The mesocosms were deployed on the bottom of the lake for either 11 (Experiment 1) or 15 (Experiment 2) days at a depth of 1 m. We left the tops of the mesocosms open to allow exchange with the ambient lake water, except during measurements of metabolism when they were sealed with rubber stoppers for several hours (see *Measurements of NEP, GPP, and RESP*). Mývatn is spring-fed and has substantial lateral water flow even on days with low wind, so there was likely significant exchange between the

mesocosms and overlying water (Bartrons et al. 2015).

Experiment 1: Mechanism of midge engineering.—We used a factorial experiment to test two mechanisms by which midges may increase ecosystem metabolism rates: (1) enhanced substrate quality by building silk tubes and (2) promoting algal growth by mobilizing nutrients. The experiment had a 2 × 2 × 2 design crossing midge presence with artificial silk structures (to mimic midge tubes) and nutrient enrichment (to mimic nutrient mobilization), and we measured the responses of GPP, RESP, and chlorophyll-a. We predicted that if tube building by midges stimulated algal growth, then the presence of either silk or midges would increase GPP by a comparable amount. However, if the benefits of enhanced sediment structure (provided by either midges or silk) saturate, then the presence of both midges and silk should be lower than what would be expected from their separate effects. Similarly, we predicted that if nutrient mobilization by midges stimulated GPP, then midges and nutrient enrichment would both increase GPP when applied separately but that these effects would be at least partially redundant when applied together. We expected RESP to respond similar to GPP, as is often the case in lake ecosystems with high in situ production. Since GPP and RESP have opposite effects on NEP, the effects of midges, silk, and nutrients would depend on the relative magnitude of their effects on GPP and RESP.

The presence of midges and associated sediment structure was manipulated as described in *Methods: Mesocosms*. To mimic midge engineering, we used thin sheets of natural silkworm silk (Undyed Silk Hankies, Yarn Designers Boutique, California, USA) originally 25 × 25 cm that we stretched into loops approximately 15 cm in diameter. Each mesocosm received a single silk loop, which we loosely coiled into a three-dimensional structure and positioned so that the bottom half of the loop sat below the sediment surface (Appendix S1: Fig. S1). While the silk coils were clearly not a perfect imitation of midge tubes, they are similar in that they provided three-dimensional structure that expanded the effective surface area available for algal growth. The silk could present a physical barrier reducing between the sediment and the water column, although this also is similar to the effect of the midge tubes and silk that can completely cover the sediment surface.

We manipulated nutrient concentration with agar rods (1.5 cm diameter × 15 cm length) either enriched with both N and P or not enriched (Tank et al. 2006) that were pushed vertically into the mesocosm sediment. While N and P are not the only nutrient that could be limited for benthic primary producers (particularly Si for diatoms; Kilham 1971, Paasche 1973), N and P are the nutrients that are most obviously influenced by midges and are also the focus of most studies of nutrient limitation in freshwater systems (Svensson and Leonardson 1996, Hölker et al. 2015). We enriched the agar with NH_4Cl and KH_2PO_4 to produce N and P concentrations of 0.5 mol/L and 0.13 mol/L, respectively, to roughly mimic the excretion ratios measured from *Tanytarsus* (Herren et al. 2017). Laboratory measurements of similarly enriched agar rods yielded average N and P release rates of 22.8 and 1.23 mg/day, respectively (Appendix S1). The rods were constructed by pouring the hot agar into clean surgical tubing cut to the appropriate length, with a bamboo skewer inserted into the center for stability.

We secured the mesocosms to two racks with 12 mesocosms each. We intended to use a balanced design with three replicates in each of eight treatment combinations (total $n = 24$). However, due to a logistical error one silk-present and silk-absent treatments were switched for each nutrient and midge combination, so that each treatment had either 2 or 4 replicates. We deployed the experiment on the lake bottom near the southern shore from 2 to 13 August 2016 and measured GPP, RESP, and NEP on the 3rd and 11th days of deployment (see *Measurements of NEP, GPP, and RESP*). On day 11, we collected 1 mL of surface sediment from each mesocosm (after removing the silk in the silk treatment) and quantified chlorophyll-a concentration extracted in methanol with a fluorometer (Turner Designs, Sunnyvale, California, USA; Welschmeyer 1994, Herren et al. 2017). We also measured the chlorophyll-a in the silk loops from each mesocosm in the silk-present treatment; chlorophyll-a was extracted from the entire silk loop using methanol, following the same procedure as for the sediment.

Experiment 2: Light mediation of midge engineering effects.—We quantified the relationship between light and midge effects on benthic production by measuring NEP across a light gradient in the presence or absence of midges with their associated engineering. The experiment consisted of 48 mesocosms filled with sieved and intact sediment (*Methods: Mesocosms*). To create variation in light, we wrapped the sides of the upper 18 cm of 40 mesocosms with 0, 1, 2, 3, or 4 layers of white mesh. We wrapped two layers of black plastic around the sides of the upper 18 cm of the remaining eight mesocosms. There was no algal growth or other fouling on the sides of the mesocosms during experiment, so the shading treatments remained consistent. Altogether, we had six shading treatments with eight replicates each. These replicates were evenly distributed across the two midge treatments, for a total of 12 treatment combinations.

We secured the mesocosms to three racks with 16 mesocosms each. Thirty-six replicates were distributed among racks in a complete block design, while the remaining 12 mesocosms were distributed haphazardly. We deployed the experiment in a small bay in the southeastern corner of Mývatn, free of the thick cyanobacterial bloom occurring across the rest of the lake that prevented most of the light from penetrating to a depth of 1 m. *Tanytarsus* and *Chironomus* are absent from this portion of the lake (due to the hard substrate) and therefore could not colonize the mesocosms. This portion of the lake is near the springs that feed the main basin, and has substantially lower N:P ratios (~1:1) than the rest of the lake (~16:1 for the outlet on the opposite side of the lake). However, the nutrient content in the sediment pore water of the mesocosms was likely much higher than in the water column, so differences in water column chemistry likely had minimal effects (Gíslason et al. 2004). The experiment was deployed from 28 July to 12 August 2015, and we measured NEP on 3rd and 15th days of deployment (see *Measurements of NEP, GPP, and RESP*).

To determine the effect of shading treatments on in situ light levels at the mesocosm sediment surface, we measured the photosynthetically active radiation (PAR) inside of a clear polycarbonate tube secured with the appropriate shading treatment. We secured a light meter (Li-192 Quantum Underwater Sensor, Li-COR, Lincoln, Nebraska, USA) 18 cm from the top of each tube and took the readings with the sensor just below the water's surface, at 0.5 below the surface, and 1 m below the surface. For each set of readings, we also measured ambient light with the meter outside of the tube. This allowed us to calculate the effect of a given shading treatment as a fraction of surface irradiance at a given depth. We repeated each series of measurements three times so we could average across changes in ambient light intensity within a series of measurements at different depths. Throughout the incubation period for measuring NEP (see *Measurements of NEP, GPP, and RESP*), we measured PAR using the bare sensor at the locations above/below the water surface as described above. This allowed us to estimate the light level experienced by each mesocosm during the incubation, given its shading treatment and the ambient light level. Estimated light levels at the sediment surface ranged from 3.43 to 228 μmol-photons·m^{-2}·s^{-1}. From our long-term sampling location in May–August 2013–2017, approximately 77% of light levels observed at midday from a depth of 2.5 m (Mývatn's average depth) were within the experimental range. Day 15 was sunnier than day 3, so the most extreme mesocosm light levels were greater for day 15, although with substantial overlap with day 3 due to the shading treatments.

To evaluate the efficacy of our midge (sieving) treatments and determine how much the larval midges grew, at the end of the experiment we sieved sediment from all cores in the full light and full dark shading treatments (n = 16) and collected the larval midges (n = 299). We identified the midges to either tribe (Tanytarsini or Chironomini) or subfamily (Appendix S1). There was minimal colonization of the mesocosms by *Micropsectra* (tribe Tanytarsini); however, the midge-absent treatment remained largely midge-free. Tanytarsini dominated the midge-present treatment. The head capsule widths and body lengths of Tanytarsini larva were measured to determine whether the midges grew throughout the experiment. We used the distribution of head capsule widths from both the experiment and the long-term data of the Tanytarsini population to define boundaries between instars (<0.15 mm for second instar, 0.15–0.24 mm for third instar, and

>0.24 mm for fourth instar). First instars were not present in the lake during the experimental period. We quantified midge growth by comparing the midge measurements from the mesocosms to those in sediment cores taken from the source location a few days before the beginning (n = 133) and on the last day of the experiment (n = 97).

Measurements of NEP, GPP, and RESP.—Ecosystem metabolism rates were quantified in each mesocosm as the difference between the final and initial dissolved oxygen concentrations per hour (g $O_2 \cdot L^{-1} \cdot h^{-1}$) over an incubation period of approximately 4 h (ProODO, YSI, Yellow Springs, Ohio, USA; Bott 2006, Herren et al. 2017). The incubations were performed on the lake bottom at a depth of 1 m, with the mesocosms sealed with rubber stoppers for the duration (stoppers lead to an approximately 10% reduction in light at the mesocosm sediment surface). The mesocosm water columns were gently stirred to homogenize the oxygen concentration before taking readings. Metabolism in the mesocosm water columns was negligible, as illustrated by experiments with similar mesocosms lacking sediment where changes in O_2 were not detectable. Therefore, we converted the differences in final and initial O_2 concentrations to fluxes of O_2 across the sediment surface (g $O_2 \cdot m^{-2} \cdot h^{-1}$) by multiplying by the depth of the mesocosm water column. We present ecosystem metabolism rates as fluxes of O_2, assuming that GPP and RESP correspond to roughly equal fluxes of C and that the net O_2 flux (NEP) is biologically meaningful (Bott 2006). We recognize that measuring metabolism through closed incubations has the potential to introduce some artifact (e.g., lag of water column mixing), but this approach has been used in previous studies (Bott 2006) and should provide a reasonable quantification of variation across treatments that is the major focus of our study.

For Experiment 1, both NEP and RESP were quantified in sequential 4-h incubations under light and dark conditions, respectively. Dark conditions were achieved by wrapping the tops of the mesocosms with four layers of black plastic, which blocked out essentially all light when the rubber stoppers were in place. Gross primary production was calculated as the summed magnitudes of NEP and RESP (since NEP = GPP − RESP; Lovett et al. 2006). The average water temperatures inside the mesocosms during the light and dark incubations were respectively 14.4°C and 15.9°C on day 3, and they were 14.7°C and 13.7°C on day 11. Average light levels at the deployment depth during the light incubation were 335 and 155 μmol-photons$\cdot m^{-2} \cdot s^{-1}$ on days 3 and 11, respectively.

For Experiment 2, we incubated each mesocosms once per measurement day with the shading treatments intact (as opposed to twice per measurement day, one light and one dark, as for Experiment 1). This allowed us to quantify NEP across a light gradient, which in turn allowed us to draw inferences about GPP and RESP across midge treatments (but not for each mesocosm separately; see Appendix S1). Average water temperatures were 9.13°C on day 3 and 10.2°C on day 15 (see above for description of light levels during Experiment 2). We note that water temperatures were lower for Experiment 2 than Experiment 1, which was reflected in lower overall metabolism rates.

Statistical methods

Statistical software.—All analyses were conducted using R version 3.4.3 (R Core Team 2016).

Experiment 1: Mechanism of midge engineering.—We fit separate linear mixed models (LMMs) for GPP, RESP, and NEP with two-way interactions between silk, midges, nutrients, and time. Mesocosm identity was included a random effect to account for repeated measures. A single extreme value was omitted for day 11, which did not alter the statistical conclusions. We calculated P-values using F-tests with the Kenward-Roger approximation, which can be applied to unbalanced designs (Luke 2017). We performed a parallel analysis to compare chlorophyll-a across treatments, although these data were only available for day 11 so there was no need to account for repeated measures. Unless otherwise noted, we reported P-values for the full models, due to the risk of inflated type I errors following model selection (Freedman 1983). However, we also dropped non-significant interactions with backward selection to check for changes in the inference for corresponding fixed effects.

Experiment 2: Light mediation of midge engineering effects.—Experiment 2 quantified NEP across a light gradient, with and without midges, and at two time points (days 3 and 15). We

analyzed these data by fitting a modified productivity–irradiance curve with a Michaelis-Menten form (Jassby and Platt 1976):

$$\mathrm{NEP}_i = \frac{\alpha_i \times \mathrm{light}_i}{1 + \beta \times \mathrm{light}_i} + \delta_i + \varepsilon_{\mathrm{rack/mescosm[i]}} \quad (1)$$

$$\alpha_i = \alpha_1 + \alpha_2 \times \mathrm{midge}_i + \alpha_3 \times \mathrm{time}_i + \alpha_4 \times \mathrm{midge}_i \times \mathrm{time}_i$$

$$\delta_i = \delta_1 + \delta_2 \times \mathrm{midge}_i + \delta_3 \times \mathrm{time}_i + \delta_4 \times \mathrm{midge}_i \times \mathrm{time}_i$$

where i is an index for observations, ε is the residual error nested within rack and mesocosm, light is the in situ light level (PAR; μmol-photons·m^{-2}·s^{-1}), midge and time are binary indicators for midge treatment and time, and α_1, α_2, α_3, α_4, β, δ_1, δ_2, δ_3, and δ_4 are parameters to be estimated. The term α_i is the maximum rate of increase in NEP, and β is the rate at which NEP saturates with increasing light. The term δ_i captures light-independent effects on NEP. The hierarchical forms of α_i and δ_i allowed us to test the effects of midge presence, time, and their interactions on the light-dependent and light-independent components of NEP. In general, the light-dependent terms should be related to GPP and light-independent terms to RESP (Attard et al. 2014), although possible changes in algal biomass or microbial activity across light treatments potentially complicate this interpretation for day 15.

We evaluated the importance of the model parameters by fitting reduced versions of the full model that excluded different parameters and then ranked the models by their AIC scores (Burnham and Anderson 2002). This resulted in 25 models comprising all combinations of midge and time effects, with the restriction that models including midge × time interactions for either α or δ also included the corresponding main effects. The models were fit using maximum likelihood, with normally distributed residuals and random effects to account for blocking (rack) and repeated measures (mesocosm). Following model selection, we refit the optimal model using restricted maximum likelihood for presentation of its results.

We quantified changes in midge stage structure by comparing the proportion of Tanytarsini individuals in second instar between the end of the experiment and (1) in-lake samples immediately prior to the experiment (to approximate the starting conditions for the experiment) and (2) in-lake samples at the end of the experiment with separate binomial generalized linear mixed models (GLMMs) including observation-level random effects to account for overdispersion. This allowed us to compare changes in midge stage structure in the mesocosms and the lake. Fewer than 5% of individuals were fourth instar, so this analysis essentially compared the proportions of second vs. third instars. To quantify midge growth, we performed a parallel analysis on body lengths using LMMs, with random effects for mesocosm or sediment core. We calculated *P*-values with either likelihood ratio tests (GLMMs) or *F*-tests using the Kenward-Roger approximation (LMMs; Luke 2017).

We used the average densities of Tanytarsini (predominantly *Tanytarsus gracilentus*) and Chironomini (*Chironomus* spp.) observed in the midge-present mesocosms to estimate the potential contribution of respiration by midges themselves to NEP. We used these two taxa because Tanytarsini composed most of the individuals in the mesocosms and *Chironomus* are much more massive than any of the other taxa and therefore would contribute disproportionately to total respiration per individual. We used measurements of individual dry weights for these two taxa from Herren et al. (2017) and literature values (Brodersen et al. 2004) for biomass-specific respiration measured at 10°C (the approximate summer average water temperature in Mývatn) to estimate total respiration for the midge densities observed in the mesocosms. We averaged different values for *Tanytarsus gracilientus* and *Chironomus* spp. (*C. hyperboreus* and *C. riparius*—values for the main *Chironomus* species in Mývatn, *C. islandicus*, were not reported). This yielded the following estimates of total taxon-specific respirations:

Tanytarsini: 118.2 individuals × 0.0769 mg/individual × 7.7 μg O_2·h^{-1}·mg^{-1} = 70.00 μg O_2/h

Chironomini: 7.5 individuals × 0.6812 mg/individual × 1.862 μg O_2·h^{-1}·mg^{-1} = 9.51 μg O_2/h

Therefore, the combined respiration of Tanytarsini and Chironomini was 79.50 μg O_2/h, or 0.0000795 g O_2/h.

Lake-scale effects of midges on NEP.—To investigate how natural variation in benthic light intensity may alter midge effects on NEP, we combined the model fit to data from Experiment 2 (Eq. 1) with field observations of light transmission to the lake bottom to project the potential spatiotemporal variation in midge effects on benthic production across the lake. The purpose of this projection was to place our experimental results in a broader context by illustrating how much variation one would expect in midge engineering effects across the lake given natural variation in light. This was in contrast to predicting the actual lake-wide effect of midges on NEP, which would require both characterizing the response of ecosystem metabolism to a gradient of midge densities and fine resolution of data on spatial variability in midge density, both of which were beyond the scope of this study.

We calculated the net midge effect as the partial derivative of Eq. 1 with respect to the binary midge index (identical to taking the difference between the equation evaluated with and without midges). For the full version of the model, the net midge effect as a function of light level and time was calculated as

$$\frac{\partial \text{NEP}}{\partial \text{midge}} = (\alpha_2 + \alpha_4 \times \text{time}) \times \text{light} / (1 + \beta \times \text{light}) + \delta 2 + \delta 4 \times \text{time} \quad (2)$$

with light as continuous variation in PAR, time as a binary indicator for the day of the experiment, and all parameters defined as above. The parameter values were based on the estimates associated with the final model as determined through the model selection procedure (terms that were not included in the final model were set to 0). Projections of midge effects at each time point were calculated by substituting light levels into this expression.

In July and August 2015, Mývatn experienced a thick cyanobacterial bloom, during which we took light readings at 65 sites around the lake to determine the local rates of light attenuation (Appendix S1). The sites were positioned on a 500 × 500 m grid, and at each site, we recorded light levels at 0.5-m intervals between the surface and 2 m. We estimated the exponential light attenuation at each site, which characterized the spatial variation in the severity of the bloom. The spatial pattern of the bloom roughly matched that from 2011 (Bartrons et al. 2015) and 2016–2017 (*unpublished data*) based on measurement of cyanobacterial pigments and cell counts. For each site, we calculated the light level on the lake bottom assuming moderate surface light of 320 μmol-photons·m^{-2}·s^{-1} and one of three water clarity scenarios: low clarity (100% measured light attenuation), medium clarity (40%), or high clarity (15%). Surface light was set to ensure that benthic light levels were within the range of observations over which the model was fit (which included approximately 77% of light levels observed at midday from a depth of 2.5 m at our long-term sampling location in May–August 2013–2017). Spatial variation in benthic light levels reflected both differences in depth and observed bloom severity. For each water clarity scenario, we quantified the site-specific midge effect by evaluating Eq. 2 for the corresponding light level. We made projections using both time points in Eq. 2, corresponding to midge communities dominated by either second- or third-instar Tanytarsini (see *Results*). This resulted in six scenarios of water clarity and midge stage.

Results

Experiment 1: Mechanism of midge engineering

Experiment 1 tested two mechanisms by which midges may stimulate GPP and RESP: enhanced substrate quality and nutrient mobilization. Gross primary production was higher in the presence of midges ($F_{1,24.78} = 6.34$, $P = 0.019$) and silk ($F_{1,25.64} = 6.83$, $P = 0.015$) than in their absence, and these effects were of comparable magnitudes (Fig. 3a, b). However, there was a significant negative interaction between these effects ($F_{1,15.33} = 16.31$, $P = 0.001$; Fig. 3a, b). While GPP was higher with both silk and midges than with neither, GPP with both was comparable to (or perhaps slightly lower than) GPP with only one or the other. This is consistent with the possibility that experimental silk and midges provide similar net benefits to GPP that saturate

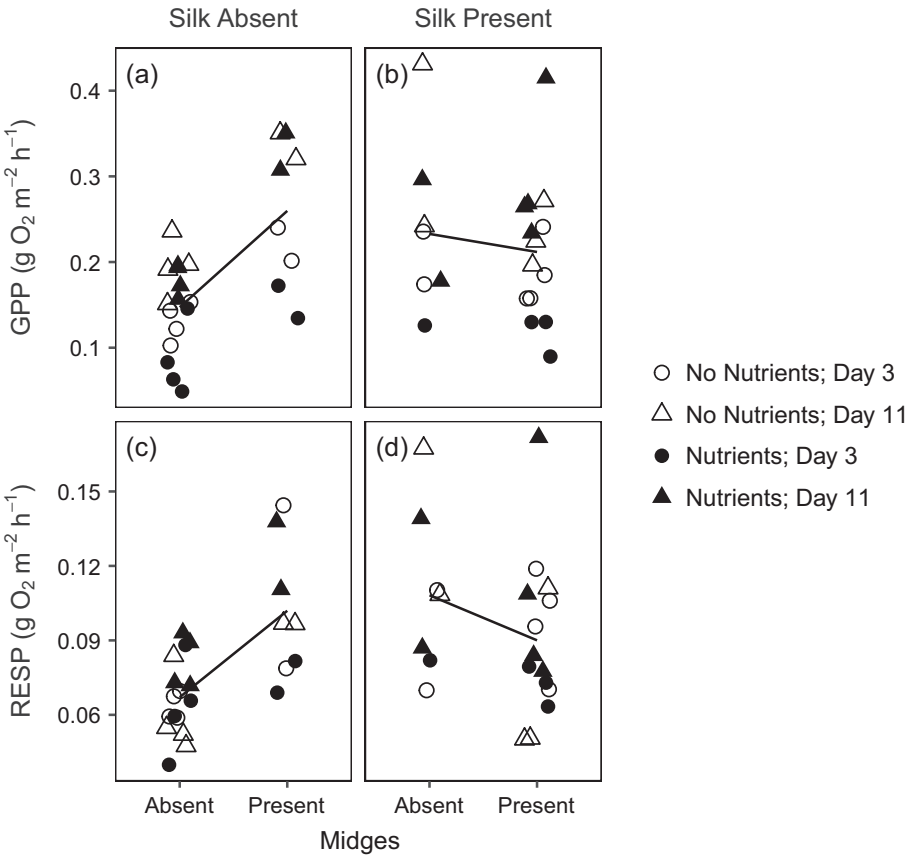

Fig. 3. Midges and silk increase gross primary production (GPP) and RESP. Each panel shows GPP (a,b) or RESP (c,d) for either absence (a,c) or presence (b,d) of silk. The data are grouped by midge treatment, nutrient treatments are represented by filled (nutrients) and open (no nutrients) points, and days are represented by circles (day 3) and triangles (day 11). Lines show fits from LMMs. Using standard photosynthetic and respiratory quotients of 1.2 and 0.85, a 0.1 g $O_2 \cdot m^{-2} \cdot h^{-1}$ O_2 difference equals 0.031 g $C \cdot m^{-2} \cdot h^{-1}$ and 0.032 g $C \cdot m^{-2} \cdot h^{-1}$, respectively.

when both are present, although it could also be due to the silk directly altering the effects of the midges. Nutrient enrichment had a negative effect on GPP ($F_{1,27.04} = 6.65$, $P = 0.016$), although it was only visually obvious in the day 3 data and was only marginally significant when non-significant interactions including nutrients were dropped. Gross primary production increased from day 3 to 11 across all treatments ($F_{1,17.90} = 5.0$, $P = 0.038$). This implies that nutrients were not limiting and therefore that nutrient mobilization could not explain the positive effect of midges on GPP in the experimental mesocosms.

Paralleling GPP, RESP increased with midges ($F_{1,24.78} = 5.85$, $P = 0.023$) and silk ($F_{1,25.64} = 5.07$, $P = 0.033$), but with a negative interaction ($F_{1,16.31} = 9.58$, $P = 0.007$; Fig. 3c, d). There was a nutrient × day interaction ($F_{1,18.95} = 5.16$, $P = 0.035$), with the nutrient effect being relatively more negative on day 3 than day 11. By definition, GPP and RESP had opposite effects on NEP, but because the overall magnitude of GPP was greater than RESP, GPP had a disproportionate influence. Therefore, the response of NEP to the experimental treatments broadly paralleled GPP, with positive effects of midges ($F_{1,24.78} = 4.33$, $P = 0.048$) and silk ($F_{1,25.64} = 5.63$, $P = 0.025$), and negative midge × silk interaction ($F_{1,15.52} = 16.31$, $P = 0.001$), and negative effects of nutrients ($F_{1,27.04} = 11.90$, $P = 0.002$; Appendix S1: Fig. S2). Net ecosystem production was higher on day 11 than day 3 ($F_{1,17.09} = 15.12$, $P = 0.001$), and there

was a positive midge × day interaction ($F_{1,18.89}$ = 4.61, P = 0.045).

Sediment chlorophyll-a was higher with midges (mean ± standard error = 21.4 ± 1.6 mg/L) than without (16.2 ± 0.8 mg/L; $F_{1,20.0}$ = 9.87, P = 0.005), although this effect was only significant when the non-significant interactions with silk and nutrients were dropped. There were no significant effects of silk ($F_{1,20}$ = 0.74, P = 0.400) or nutrients ($F_{1,20}$ = 0.15, P = 0.706) on chlorophyll-a in the sediment itself (i.e., with the silk removed; P-values for the reduced model). On the silk itself, chlorophyll-a concentrations were >10 times (254 ± 50 mg/L) than in the sediment (regardless of silk treatment).

Experiment 2: Light mediation of midge engineering effects

Experiment 2 quantified the net effect of midges on benthic NEP across a light gradient. We fit models (Eq. 1) of in situ NEP with different combinations of midge and time effects on light-dependent and light-independent processes. Of the 25 possible models, the three best were similarly well supported (ΔAIC < 2), and all remaining models had ΔAICs > 4 (Table 1). For simplicity, we present the results from the second-best model as it had the fewest parameters, noting that each of the three best models provides similar interpretations of the data. The second-best model contained a light-dependent main effect of midges (slopes in Fig. 4) and light-independent main and interaction effects of midges and time (y-intercepts in Fig. 4).

Table 1. AIC values for models of NEP (Eq. 1) fit to data from Experiment 2.

Light-dependent (α) fixed effects	Light-independent (δ) fixed effects	Number of fixed effects parameters	AIC	ΔAIC
midge + time	midge × time	8	−474.67	0.00
midge	midge × time	7	−473.17	1.50
midge × time	midge × time	9	−472.69	1.99
midge × time	midge + time	8	−470.25	4.42
midge × time	time	7	−465.31	9.36

Notes: The models vary by light-dependent (α) and light-independent (δ) effects of midge treatment and time. Models with interactions (×) also include corresponding main effects. All models include the saturation parameter β and intercepts for α and δ; 1 indicates intercept only. For clarity, only models with ΔAIC < 10 are shown (see Appendix S1: Table S3 for details on all models).

Midges enhanced NEP at high light levels through their positive effect on GPP, but this effect declined as light decreased to levels too low to sustain algal photosynthesis (Fig. 4). Furthermore, midges increased RESP, such that their net effect on NEP switched from positive to negative at low light levels. The direct contribution of midge respiration to total respiration was likely small (estimated as 0.0000795 g O_2/h, while the difference in NEP between midge-present and midge-absent treatment in the dark was −0.044 g O_2/h), indicating that midges stimulated respiration of other organisms in the sediment. Net ecosystem production in the midge-absent mesocosms did not change between the beginning and end of the experiment (Appendix S1: Fig. S3), indicating an absence of transient artificial effects of the manipulation (i.e., sieving sediment) per se. In contrast, NEP declined substantially through time in the presence of midges, which resulted from an increase in midge stimulation of RESP (y-intercepts in Fig. 4) while the midge effect on GPP (slopes in Fig. 4) remained the same. Consequently, the amount of light required for the positive effects of midges on NEP to outweigh the negative effects was substantially higher at the end of the experiment (91 μmol-photons·m^{-2}·s^{-1}) than at the beginning (8 μmol-photons·m^{-2}·s^{-1}).

The change in midge effects on NEP through time coincided with a shift in midge stage structure (χ^2 = 13.35, df = 1, P = 0.0003). At the beginning of the experiment, 26.3% of Tanytarsini larvae were third instar, while 72.2% were third instar by the end. Slightly more Tanytarsini were third instar in the lake (88.7%) than in the mesocosms at the end of the experiment, but this difference was not significant (χ^2 = 2.16, df = 1, P = 0.141). Tanytarsini body lengths exactly paralleled these results. The midges grew between the beginning (mean length = 2.42 mm) and end (2.70 mm) of the experiment ($F_{1,11.3}$ = 5.34, P = 0.041), and were not significantly longer in the lake than in the mesocosms at the end (mean = 3.10 mm; $F_{1,11.68}$ = 3.82, P = 0.075). Approximating individual midges as cylinders and using the head capsule width as a proxy for diameter, the midges nearly doubled in volume (and therefore body mass) over the course of the experiment (Appendix S1).

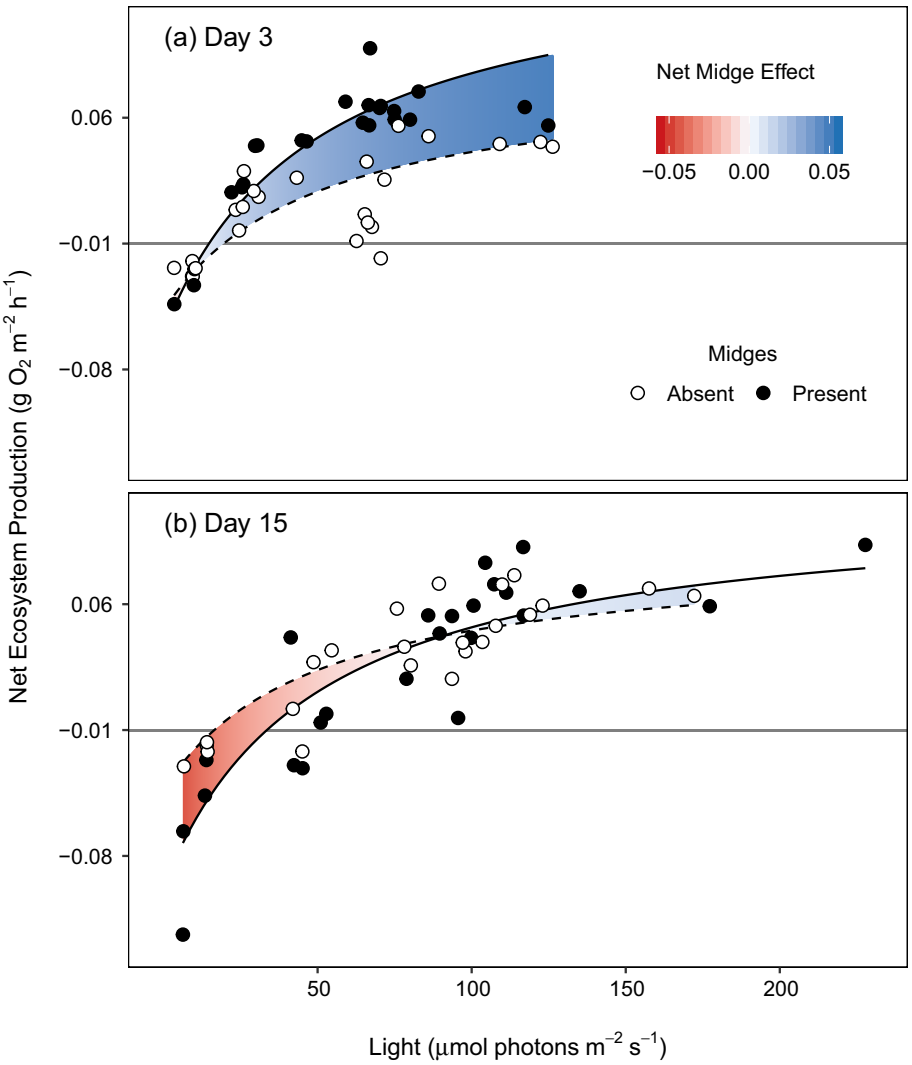

Fig. 4. Light mediates midge effects on benthic net ecosystem production. Net ecosystem production from Experiment 2 is plotted against light for (a) day 3 and (b) day 15. The lines show model estimates evaluated with (solid) and without (dashed) midges. The colored shading indicates the net midge effect, calculated as the difference in the model estimates when evaluated with and without midges. The shift between days 3 and 15 is associated with a shift from second- to third-instar midges. Using a photosynthetic quotient of 1.2, a net midge effect of 0.1 g $O_2 \cdot m^{-2} \cdot h^{-1}$ equals 0.031 g $C \cdot m^{-2} \cdot h^{-1}$.

Lake-scale effects of midges on NEP

We used Eq. 2 and field measurements of light attenuation during a cyanobacterial bloom to project potential midge effects on production across the lake. Based on the model selection described above, we employed the parameterization of the model that excluded the light-dependent midge × light interaction (α_4), yielding the following expression for the net midge effect

$$\frac{\partial \text{NEP}}{\partial \text{midge}} = \alpha_2 \times \text{light}/(1 + \beta \times \text{light}) + \delta 2 + \delta 4 \times \text{time} \quad (3)$$

where $\alpha_2 = 0.00169$ [(g $O_2 \cdot m^{-2} \cdot h^{-1}$/µmol-photons·$m^{-2} \cdot s^{-1}$)], $\beta = 0.0202$ [1/(µmol-photons·$m^{-2} \cdot s^{-1}$)], $\delta_2 = -0.0122$ [g $O_2 \cdot m^{-2} \cdot h^{-1}$], and $\delta_4 = -0.0420$ [(g $O_2 \cdot m^{-2} \cdot h^{-1}$)/$time^{-1}$]. We made projections for low (100% observed light attenuation), medium

(40%), and high (15%) water clarities crossed with two dominant midge stages (second and third instar, corresponding to days 3 and 15 of Experiment 2). Across the six scenarios, projected midge effects on benthic NEP ranged from strongly negative (-0.054 g $O_2 \cdot m^{-2} \cdot h^{-1}$) to strongly positive (0.053 g $O_2 \cdot m^{-2} \cdot h^{-1}$), thus spanning ~0.11 g $O_2 \cdot m^{-2} \cdot h^{-1}$ (Appendix S1: Fig. S6). The estimated seasonal production by diatoms from Mývatn (200 g C/m^2) in a year of moderate midge abundance (Jónasson 1979) converted to the same timescale and units is roughly 0.22 g $O_2 \cdot m^{-2} \cdot h^{-1}$ (Appendix S1), which means that the potential range of projected midge effects is substantial relative to the overall magnitude of production. In some cases, both moderately positive and moderately negative midge engineering effects occurred across the lake for a given water clarity scenario (Fig. 5). Spatial variation was highest at medium water clarities, while midge effects at extreme water clarities tended to be either uniformly positive, negative, or neutral across the lake.

Discussion

Our results show how environmental conditions can alter the magnitude and sign of ecosystem engineer effects on their ecosystems: Midges acting as both engineers and consumers increase benthic NEP when light is abundant but decrease NEP when light limits algal photosynthesis. Mývatn experiences patchy and episodic cyanobacterial blooms, which generate large variation in water clarity and benthic light levels across the lake, within a season, and between years. Therefore, the influence of midge ecosystem engineering on benthic production is spatiotemporally complex, and the positive effects of midges can be overshadowed by events in the pelagic zone. The majority of the world's lakes are shallow and likely to be limited by light (Karlsson et al. 2009, Cael et al. 2017), which is of increasing concern given increasing eutrophication and associated declines in water clarity (Vadeboncoeur et al. 2003, Taranu et al. 2015). Our results have implications for how such changes may produce spatiotemporal variation in the effects of benthic ecosystem engineers on the function of a variety of aquatic ecosystems.

We tested two hypothesized mechanisms for positive midge effects on benthic production at high light levels: (1) enhanced substrate quality by building silk tubes and (2) increased nutrient availability by mobilizing N and P. Experiment 1 supported the first hypothesis and rejected the second. Artificial silk structures increased GPP in midge-absent mesocosms to a level similar to the midge-present mesocosms without silk. However, addition of silk to midge-present mesocosms caused no further increase in GPP, suggesting that the potential benefit of artificial silk was already provided by the tubes and silk webs constructed by the midges (although this silk could also have had direct effects on the midges or their effects on GPP). Furthermore, chlorophyll-a was higher in the presence of midges and silk (on the silk itself), so it is likely that higher algal biomass supported by the enhanced substrate contributed to higher GPP (Pringle 1985). In contrast, addition of nitrogen and phosphorus slightly reduced GPP, implying that the algae were not strongly limited by those nutrients and hence would not benefit from nutrient mobilization by midges. The negative effect of nutrient enrichment could be due to a shift in the algal community (e.g., from diatom to green algae dominated; Steinman et al. 2016) or from artifacts of the agar preparation such as release of hydrogen peroxide (Tanaka et al. 2014). An additional caveat is the potential for benthic production to be limited by nutrients other than N and P (e.g., Si for benthic diatoms; Kilham 1971, Paasche 1973), although these two elements are the nutrients that are most obviously influenced by midges (Hölker et al. 2015) and are also the focus of many studies of nutrient limitation in freshwater systems (Elser et al. 2007).

The negative effect of midges on NEP at low light levels resulted from their effect on total respiration. In both experiments, midges increased total respiration, yet respiration by midges themselves likely made a small contribution to this effect. Bioturbation by midges and other sediment-dwelling invertebrates can stimulate aerobic respiration by microbes through oxidizing the sediment and shifting bacterial community composition (Yeager et al. 2001, Hölker et al. 2015, Baranov et al. 2016*a*, *b*). Furthermore, defecation by midges could provide a carbon substrate for microbial respiration (Svensson and Leonardson 1996). Midge effects on RESP increased throughout Experiment 2, causing the apparent effect of midges on NEP to become less positive or more negative. This change was

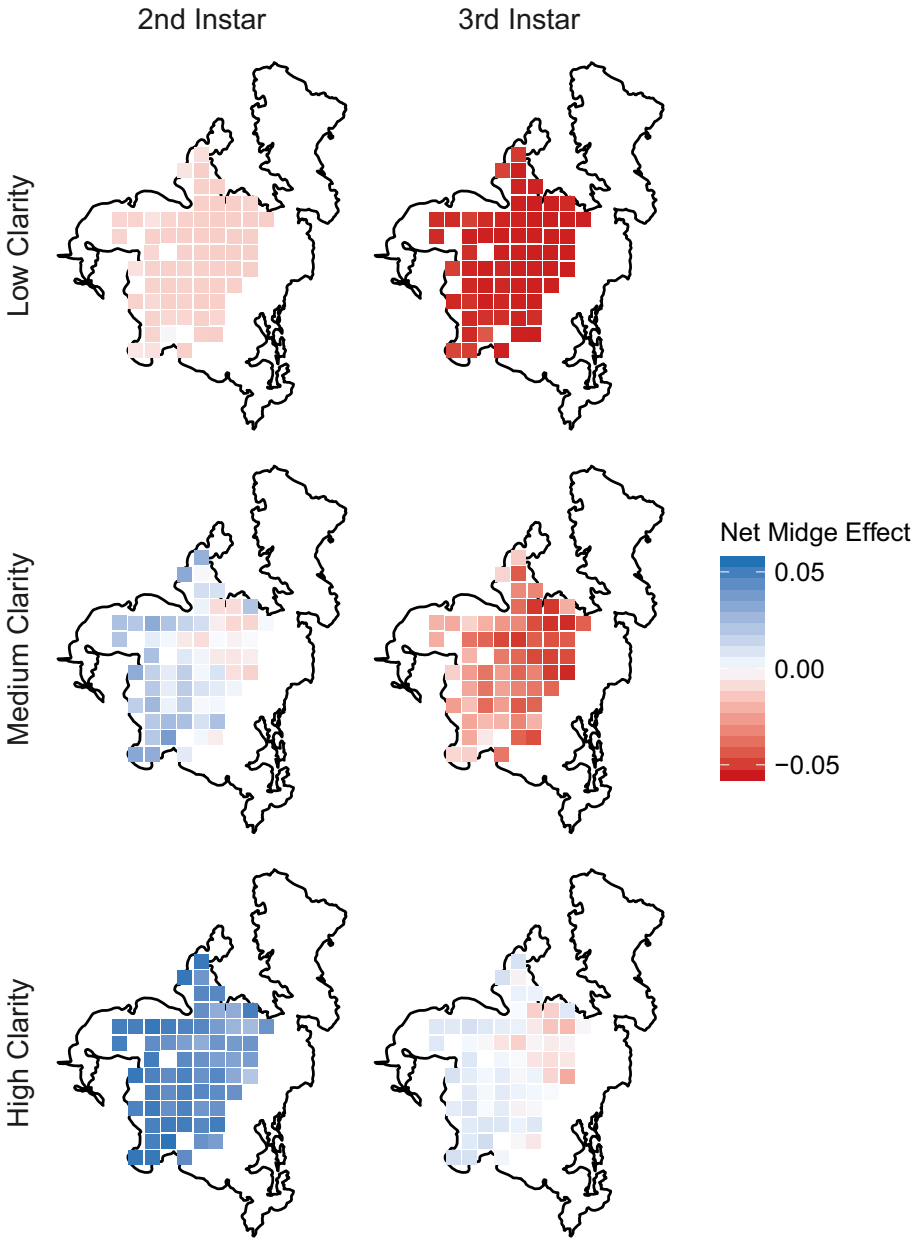

Fig. 5. Projected midge effects on net ecosystem production (NEP) vary through space and time. The maps show projected effects of midges on NEP across Mývatn. Midge effects were calculated as the difference in the model estimates when evaluated with and without midges. Different panels correspond to benthic light levels for the different water clarity scenarios (low, medium, and high) and Tanytarsini stages (second and third instar dominated). Using a photosynthetic quotient of 1.2, a net midge effect of 0.1 g $O_2 \cdot m^{-2} \cdot h^{-1}$ equals 0.031 g $C \cdot m^{-2} \cdot h^{-1}$.

accompanied by a large shift in size- and age-structure of the midge populations; the midges shifted from second to third instar dominated and nearly doubled in body mass. Larger midges may have increased bioturbation to meet their higher metabolic demands, further oxygenating the sediment and stimulating greater respiration (Hölker et al. 2015, Baranov et al. 2016*a*, *b*).

By quantifying the functional dependence of the ecosystem engineering on continuous environmental variation, we were able to illustrate the expected spatiotemporal variation in the effects of midge engineering due to natural variation in light. These projections illustrate the potential for realistic variation in environmental conditions to produce large variation in engineer (e.g., midge) effects through space (across the lake) and time (between periods with and without cyanobacterial blooms). Cyanobacteria have many impacts on aquatic ecosystems that could affect benthic production beyond simply limiting light, such as nitrogen fixation and release of toxins (Elser 1999, Dokulil and Teubner 2000). Nonetheless, our projections illustrate one key respect in which cyanobacterial blooms could result in spatiotemporal variation in the effects of midge engineering on benthic production. While our analysis focused on the role of environmental variation in producing variation in engineer effects, the density of engineer populations is itself variable and likely to have large consequences for predicting engineer effects (Hastings et al. 2007). For example, *Tanytarsus* in Mývatn fluctuate across five orders of magnitude among years, with erratic population crashes that are difficult to anticipate (Ives et al. 2008). Given the large magnitude of their effects on benthic ecosystem processes, these fluctuations in abundance likely have large consequences for the whole system. While Mývatn is a fairly extreme example, many other ecosystem engineers show large spatiotemporal variation in abundance (Nalepa et al. 1993, Bos et al. 2007). Furthermore, the effects of ecosystem engineering can feed back to the engineer populations themselves (e.g., by affecting production of their food), and the strength and duration of these feedbacks could alter the qualitative nature of their dynamics (Hastings et al. 2007, Cuddington et al. 2009, Largaespada et al. 2012). Quantifying these feedbacks is essential to predicting the consequences of environmental variation through space and time, both in Mývatn and in other cases of ecosystem engineering.

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Data Availability

Code and data can be found at https://github.com/jsphillips2/midge_light.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2760/full