

Positive feedback between chironomids and algae creates net mutualism between benthic primary consumers and producers

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Abstract. The chironomids of Lake Mývatn show extreme population fluctuations that affect most aspects of the lake ecosystem. During periods of high chironomid densities, chironomid larvae comprise over 90% of aquatic secondary production. Here, we show that chironomid larvae substantially stimulate benthic gross primary production (GPP) and net primary production (NPP), despite consuming benthic algae. Benthic GPP in experimental mesocosms with 140,000 larvae/m² was 71% higher than in mesocosms with no larvae. Similarly, chlorophyll *a* concentrations in mesocosms increased significantly over the range of larval densities. Furthermore, larvae showed increased growth rates at higher densities, possibly due to greater benthic algal availability in these treatments. We investigated the hypothesis that larvae promote benthic algal growth by alleviating nutrient limitation, and found that (1) larvae have the potential to cycle the entire yearly external loadings of nitrogen and phosphorus during the growing season, and (2) chlorophyll *a* concentrations were significantly greater in close proximity to larvae (on larval tubes). The positive feedback between chironomid larvae and benthic algae generated a net mutualism between the primary consumer and primary producer trophic levels in the benthic ecosystem. Thus, our results give an example in which unexpected positive feedbacks can lead to both high primary and high secondary production.

Key words: benthic primary production; consumer-resource dynamics; facilitation; nutrient cycling; positive feedback.

INTRODUCTION

Predation is classically defined as an interaction where a consumer species exerts a net negative effect on a resource's per-capita growth rate while receiving a net benefit from exploiting the resource population (Gotelli 2001). However, these long-term emergent effects on population growth rates are the result of many discrete, short-term interactions (Vázquez et al. 2015). During these short-term interactions, one species can exert either positive or negative effects on another species (Chamberlain and Holland 2009). For example, individuals from two species may experience a range of different interactions based on environmental factors (Juliano 2009), the abundance of other species (Paine 1969), or life stage (Pimm and Rice 1987). Thus, although consumers generally suppress resource abundance (Sih et al. 1985), they may also have short-term positive interactions with their resources.

Several studies have shown that consumers can have positive effects on their resources, often in the form of

increased resource productivity (e.g., per-capita birth rate). Instances where this positive effect has been demonstrated include consumer-driven nutrient availability (McNaughton 1983, McIntyre et al. 2008, Knoll et al. 2009) compensatory plant growth following herbivore browsing (Petelle 1982), and in the context of optimum sustainable yield of fisheries (Beverton and Holt 1957). Examples where consumers might increase resource abundance are less common, but have been shown when predation shifts the resource age structure to have fewer adults and more juveniles (Zipkin et al. 2008). Still, empirical cases of positive feedbacks between consumers and food resources are scarce in comparison to the range of circumstances where they are predicted from theoretical models (Abrams 2009). Additionally, given the relatively little conceptual development of mutualistic interactions (Vázquez et al. 2015), it is unclear how this positive feedback within consumer-resource interactions might influence emergent properties such as population dynamics or ecosystem productivity.

Lake Mývatn is an anomaly for a subarctic lake, with an abundant and diverse food web (Einarsson et al. 2004). Despite a short growing season and cool temperatures, the lake has surprisingly high primary and

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secondary productivity for its high latitude (Lindegaard and Jónasson 1979). The most striking example of this high productivity are the chironomids (Diptera: Chironomidae) that can occur at densities $>500,000/m^2$ in the benthos (Thorbergsdóttir et al. 2004). Chironomid populations at Mývatn fluctuate over 3–4 orders of magnitude but routinely reach very high densities, comprising $>90\%$ of secondary production (Einarsson et al. 2002, Ives et al. 2008). It is evident that, in supporting this amount of chironomid biomass, algal growth rates are able to keep pace with the grazing pressure of these primary consumers.

We hypothesize that chironomid larvae, in addition to being consumers of the benthic algae in Lake Mývatn, also have a strong positive effect on algal productivity. We hypothesize that primary production and algal biomass increase in response to high larval densities, creating a positive feedback within this consumer-resource system. Furthermore, we hypothesize that the positive feedback might be sufficiently strong as to increase secondary production due to a higher short-term growth rate of chironomid larvae (i.e., body size increases) as their resource availability increases. We investigate two related mechanisms that could lead to this positive effect of primary consumers on primary producers: larval tubes provide a superior substrate for benthic algal growth (Pringle 1985), and larval excretion increases the availability of limiting nutrients (Atkinson et al. 2013). We hypothesize that the positive effect of chironomid larvae on their food resources is one factor that contributes to the high primary and secondary productivity of the Lake Mývatn system.

METHODS

Lake mesocosms across a range of larval densities

If chironomid larvae facilitate algal production, then we would expect that as larval densities increase, so would benthic gross primary production (hereafter, benthic GPP). This experiment was designed to determine how varying densities of chironomid larvae affect benthic algal productivity, chlorophyll *a* concentration, and growth rates of chironomid larvae. We collected chironomid larvae and sediment from Lake Mývatn using an Ekman grab on 11–14 July 2014. We identified and sorted 23,450 live chironomid larvae for this experiment. Larvae were identified to tribe, and chironomini and tanytarsini were collected for the experiment. At the collection location, almost all chironomini were *Chironomus islandicus* (Kieffer) larvae, and almost all of the tanytarsini were *Tanytarsus gracilentus* (Holmgren) larvae; therefore, we will refer to the chironomini as *C. islandicus* and the tanytarsini as *T. gracilentus*.

On 15 July 2014, we set up 55 mesocosms stocked with sieved (125 μ m) lake sediments and with eight levels of chironomid densities. Mesocosms consisted of 1-L clear polypropylene deli cups (10.4 cm diameter and 16 cm

height) filled to a depth of 10 cm with sieved sediment and left uncovered at the top. We filled mesocosms with assemblages of 75% *C. islandicus* larvae and 25% *T. gracilentus* larvae, as that was the ratio of larvae recovered from Ekman grabs. These two taxa comprised the overwhelming majority ($>95\%$) of organisms recovered from Ekman grabs. Both *C. islandicus* and *T. gracilentus* are vertical tube-building chironomids that feed non-selectively on detritus and diatoms present at the sediment surface and on their larval tubes (Einarsson et al. 2004). The two species are primarily differentiated in their ecology by size (*C. islandicus* is the larger species, averaging nine times the mass of *T. gracilentus* larvae during this study) and depth of burrows; *T. gracilentus* often builds tubes that are 2–3 cm in length near the sediment surface (Ólafsson and Paterson 2004), but we often observed *C. islandicus* building vertical burrows that extended to between 10–15 cm depth. The bioturbation activities of both species include ventilation of their blind-end burrows and particle reworking that results in biodiffusion (sensu Kristensen et al. 2012). We used the following larval densities for experimental mesocosms: 0, 50, 100, 200, 400, 600, 800, and 1200 per mesocosm. These numbers correspond to the following densities of larvae/ m^2 : 0, 5,886, 11,772, 23,544, 47,087, 70,631, 94,174, and 141,262. The amount of biomass introduced in the mesocosms with 1200 larvae was intended to exceed the maximum larval biomass that has been observed in lake sediments (Thorbergsdóttir et al. 2004). There were six replicates of the treatment with 0 larvae and seven replicates of all other treatments. We randomly distributed the mesocosms across 11 metal racks and set them on the lake bottom in an area of the lake that was 3.5 m deep, almost the maximum natural lake depth.

On 27 July 2014 (12 d later), we retrieved the mesocosms and performed incubations to analyze benthic GPP and benthic NPP of algae in the mesocosm sediments. Two mesocosms of each treatment were incubated in dark conditions (by wrapping mesocosms with shading tarp), and the remaining mesocosms were incubated under light conditions, which consisted of placing racks at a depth of 1–2 m in the lake to prevent light limitation of photosynthesis. During the incubations, we sealed mesocosms with Parafilm for a duration of 4 h. We measured the dissolved oxygen concentration in the water column of each mesocosm (mean height and volume of water column = 6.3 cm, 535 mL) before and after the sealed incubation using a YSI ProODO probe (Yellow Springs, Ohio, USA). We gently mixed the water column with the probe to homogenize any potential vertical gradients in dissolved oxygen. Benthic NPP was measured as the net oxygen change in light-incubated mesocosms. Benthic GPP was estimated using the net change in oxygen concentrations in light-incubated mesocosms plus the average oxygen consumption in the dark-incubated mesocosms of the same larval density (Vander Zanden et al. 2006). More of the mesocosms were incubated under light conditions than dark

conditions because pilot studies indicated that light-incubated mesocosms had more variable oxygen measurements than dark mesocosms. We used linear mixed models (using fixed and random effects) to analyze benthic GPP and NPP of the mesocosms. The fixed effect was the number of larvae in the mesocosms, and the random effect was the rack where the mesocosm was situated.

Immediately after benthic GPP incubations were completed, we took sediment samples of the top 0–1 cm of the mesocosms and froze them at -20°C . Within 3 weeks, sediments were analyzed for chlorophyll *a* content. We analyzed chlorophyll *a* concentration by extracting 1 mL of sediment in methanol for 24 h before quantifying fluorescence using standard protocols (Welschmeyer 1994) with a tabletop fluorometer (Turner Designs, Sunnyvale, CA, USA). We used a linear model to analyze the chlorophyll *a* content of the mesocosms as a function of the number of larvae in the mesocosms. Additionally, we used a linear model to analyze how chlorophyll-specific GPP (defined as the GPP of a mesocosm divided by the chlorophyll *a* concentration in the mesocosm) changed in response to larval density.

After chlorophyll *a* samples were taken, we then collected the chironomid larvae from the mesocosms to obtain the average dry weight of larvae in each mesocosm. The majority of remaining larvae were *C. islandicus*, because most *T. gracilentus* had pupated and emerged during the experiment. We placed these larvae in tap water at 4°C for 36 h to allow them to void their gut contents. Then, we haphazardly sampled 30 *C. islandicus* larvae from each mesocosm (or, all remaining *C. islandicus*, in the case of some of the mesocosms beginning with 50 larvae) and dried the larvae at 60°C for a minimum of 24 h to obtain an average larval dry weight for each mesocosm (Dermott and Paterson 1974). Prior to the beginning of this experiment, we had weighed a random subsample of 100 *C. islandicus* individuals to estimate initial larval weight. We used a linear model to analyze the dry weight of *C. islandicus* larvae as a function of the number of larvae stocked in the mesocosms.

Lake mesocosms for larval tubes

We hypothesized that the silken protective tubes spun by the larvae would contain elevated levels of chlorophyll *a*, as compared to loose sediments, because of the high substrate quality of larval tubes (Pringle 1985). On 12 July 2014, we used similar protocols as described earlier (larval density experiment) to establish mesocosms with chironomid larvae separated to species. These mesocosms were constructed using 400 mL containers (7.0 cm diameter) filled with approximately 275 mL of sieved sediment to a depth of 8 cm. We filled eight mesocosms with 175 larvae of *Chironomus islandicus*, eight mesocosms with 175 larvae of *Tanytarsus gracilentus*, and 10 mesocosms with no larvae. We placed mesocosms on racks and submerged them at 3.5 m depth in Lake

Mývatn. On 21 July 2014 (9 d), we retrieved the mesocosms and sampled the top 1 cm of all mesocosms for chlorophyll *a* content. We sampled chironomid tubes from the two species by collecting 0.5 mL of larval tubes. To collect the tubes, we used forceps to remove adjacent sediments and extracted the top 1 cm of the tube. We compared chlorophyll *a* content in larval tubes of each species to the chlorophyll *a* content in adjacent loose sediments.

Quantification of larval excretion

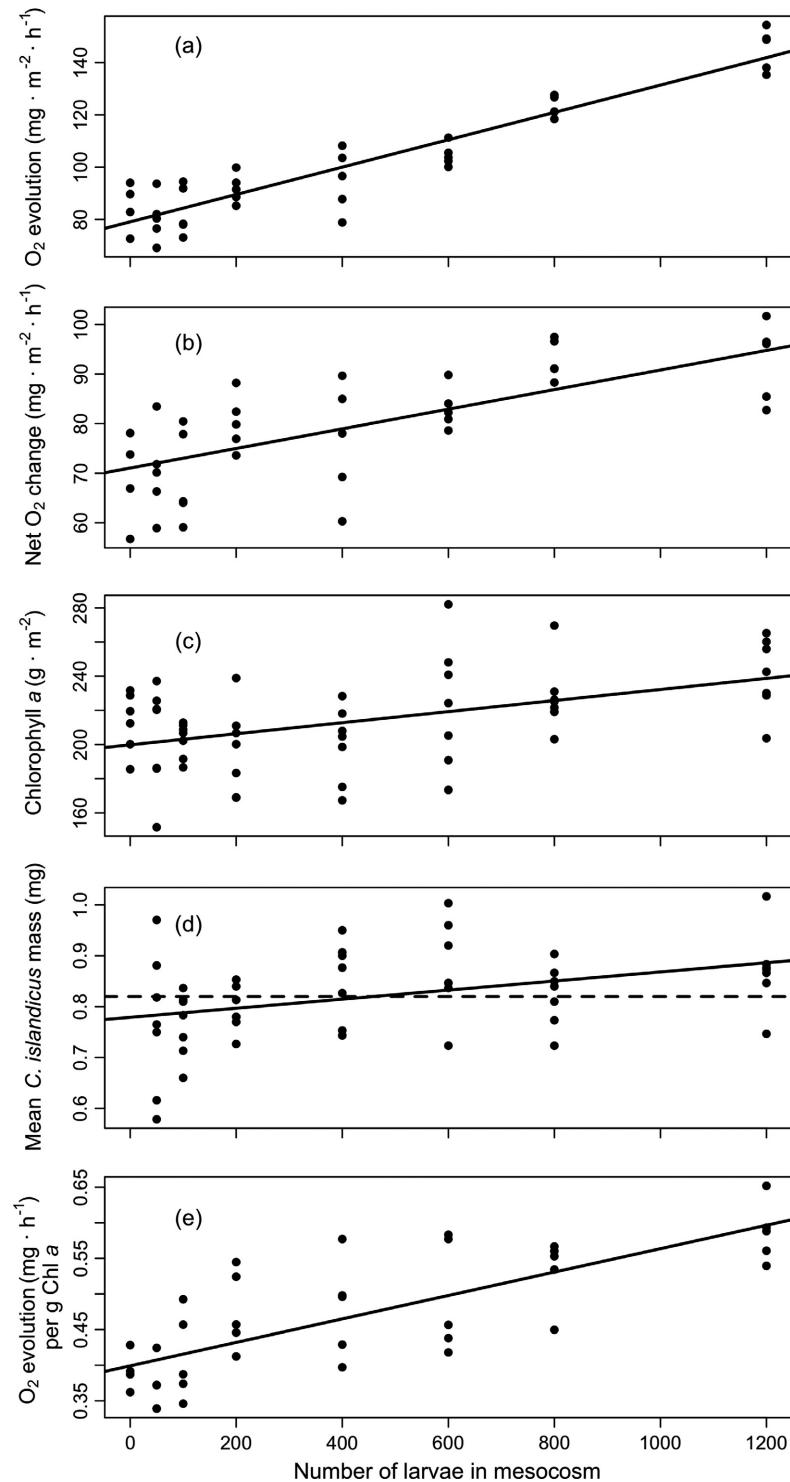
A hypothesis regarding the mechanism of the positive feedback between chironomid larvae and benthic algae was that the larvae increase nutrient availability to the algae. To investigate the magnitude of the soluble nutrient flux, we conducted incubations of chironomid larvae to quantify the amount of nitrogen and phosphorus in larval excretions.

We collected larvae with Ekman grabs on 22 July 2014. We transported the larvae back to the lab, where groups of 100 larvae were collected and immediately placed into 100 mL of distilled water in new, amber Nalgene bottles. We incubated these larvae in the shade outside for 4 h. Temperatures during the incubations were between 15.8 – 18.0°C , which is within the range of observed summer water temperatures in Lake Mývatn. Immediately afterwards, we sieved the contents of the bottles through $63\ \mu\text{m}$ mesh to remove chironomid larvae and any fecal material they had passed before obtaining larval dry weight (Dermott and Paterson 1974). The water samples from these incubation experiments were then frozen at -20°C and were transported on dry ice to Madison, Wisconsin, USA, where samples were analyzed for soluble nitrogen (combined NH_4 , NO_3^- , NO_2^-) and soluble reactive phosphorus (SRP) following protocols used by the North Temperate Lakes Long Term Ecological Research program (www.lter.limnology.wisc.edu). All statistical analyses in this study were performed with the R programming environment (v. 3.1.3), using the *base* and *stats* packages for data handling and linear regression, the *lme4* package for linear mixed models, and the *outliers* packages for detecting anomalous data points.

RESULTS

Lake mesocosms across a gradient of larval densities

Benthic GPP in mesocosms responded strongly and positively to the presence of chironomid larvae ($n = 39$, $t = 17.8$; $P < 0.001$, conditional $R^2 = 0.93$, Fig. 1a). Furthermore, there was also an increase in NPP with increasing numbers of chironomid larvae ($n = 39$, $t = 7.64$; $P < 0.001$, Fig. 1b). Thus, there were greater absolute oxygen concentrations in mesocosms with high densities of chironomid larvae, despite the increased oxygen consumption by microbes that are stimulated by larval



activity and, to a lesser extent, respiration of the larvae themselves (Baranov et al. 2016). We assumed that mortality of larvae among treatments was small and not substantially different by treatment, as differences in larval densities across treatments were still visually obvious when the mesocosms were retrieved.

Chlorophyll *a* concentrations increased linearly in response to higher densities of chironomid larvae ($F_{1,53} = 15.4$, $P < 0.001$, Fig. 1c). For every 100 larvae added to a mesocosm, chlorophyll *a* concentrations increased by 1.5% relative to mesocosms with no larvae, with no apparent saturation over the densities used in this study.

FIG. 1. (a) Benthic gross primary production (estimated from O_2 production) in 55 experimental mesocosms (39 light and 16 dark) increases across the range of initial chironomid larval densities. Each point represents the oxygen production in a light-incubated mesocosm, measured on day 13 of the study. The solid line shows the linear relationship from the mixed model fitting the oxygen production of each mesocosm as a function of the initial number of chironomid larvae in a mesocosm. (b) Net oxygen change in the light-incubated mesocosms was used to estimate NPP in the mesocosms. These rates of change in oxygen concentrations were plotted against the number of larvae originally in each mesocosm. The solid line shows the linear fit of the mixed model predicting net oxygen change as a function of the number of chironomid larvae. (c) We obtained chlorophyll *a* concentrations from the top 0–1 cm of sediments from the 55 experimental mesocosms. A linear model shows that chlorophyll *a* concentrations from experimental mesocosms increased significantly in response to higher numbers of chironomid larvae in the mesocosms (solid line). (d) We calculated the average dry mass of *C. islandicus* individuals (based on 30 haphazardly selected larvae) from each mesocosm containing chironomid larvae ($n = 49$ mesocosms). The dashed line shows the average initial dry weight of larvae before the start of the experiment (0.82 mg/individual). The solid line shows the fit of the linear model using the initial number of larvae as the predictor of *C. islandicus* final larval mass. (e) The rate of oxygen production per gram chlorophyll *a* in the light-incubated mesocosms increases as a function of the initial number of chironomid larvae in the mesocosm. The solid line shows the fit of the linear model using the number of chironomid larvae in each mesocosm as a predictor of oxygen production per gram of chlorophyll *a*.

The average individual mass of *C. islandicus* larvae increased significantly in response to higher densities of larvae stocked in the mesocosms ($F_{1,47} = 8.23$, $P = 0.0062$). That is, larvae stocked at high densities had grown more than larvae stocked at lower densities (Fig. 1d). Furthermore, average mass of larvae stocked at low densities decreased from the average starting mass (Δ dry weight = -0.052 mg for the lowest density of 50 larvae), whereas larvae stocked at high densities increased in average mass (Δ dry weight = $+0.053$ mg DW for the highest density of 1200 larvae, approximately $+6\%$ increase).

Chlorophyll-specific GPP strongly increased ($F_{1,37} = 53.0$, $P < 0.001$) in response to larval density (Fig. 1e). Thus, benthic GPP increased at a faster rate than chlorophyll *a* concentration with increasing larval densities.

Lake mesocosms for larval tubes

Chironomid tubes of both species had more than double the chlorophyll *a* concentrations of adjacent loose sediments. For mesocosms containing *T. gracilentus*, larval tubes had significantly greater chlorophyll *a* concentrations (mean \pm standard error = 51.2 mg/L \pm 2.63 mg/L), than loose sediments (mean = 22.8 mg/L \pm 1.75 mg/L, $F_{1,16} = 117$, $P < 0.001$). Similarly, *C. islandicus* tubes had a mean chlorophyll *a* concentration of 47.0 mg/L (± 2.38 mg/L) and sediments had 21.8 mg/L (± 1.58 mg/L, $F_{1,16} = 112$, $P < 0.001$). However, tubes of the two species did not have significantly different chlorophyll *a* concentrations ($F_{1,14} = 1.38$, $P = 0.26$).

Quantification of larval excretion

We obtained measurements of soluble nitrogen (combined NH_4^+ , NO_3^- , and NO_2^-) and soluble reactive phosphorus (SRP) for five incubations of *T. gracilentus* and four incubations of *C. islandicus*, after removing 1 outlier sample. Of the soluble N, 94% was in the form of NH_4^+ . For soluble N, *C. islandicus* individuals excreted 1.05 μ g/d (± 0.19 SEM), whereas *T. gracilentus* individuals excreted 0.38 μ g/d (± 0.17). However, when standardized by dry weight, *C. islandicus* excreted 1.54 μ g·d⁻¹·mg⁻¹ (± 0.82) and *T. gracilentus* excreted 4.94 μ g·d⁻¹·mg⁻¹ (± 0.73). For SRP, these values were 0.26 μ g/d (± 0.020) for *C. islandicus*

individuals and 0.10 μ g/d (± 0.018) for *T. gracilentus* individuals. By dry weight, the equivalent excretion rates were 0.37 μ g·d⁻¹·mg⁻¹ (± 0.055) for *C. islandicus* and 1.32 μ g·d⁻¹·mg⁻¹ (± 0.050) for *T. gracilentus*.

DISCUSSION

Our results indicate that chironomid larvae can generate a net positive effect on their algal resources. Despite the fact that benthic algae are a primary food source for chironomid larvae (Ingvason et al. 2004), benthic algae were more abundant and more productive with higher numbers of chironomid larvae stocked in our mesocosms. In mesocosms with 1200 larvae, benthic GPP was, on average, 71% greater than in mesocosms with no larvae. Additionally, benthic algal biomass (assessed by chlorophyll *a*) was greater in mesocosms that had been stocked with more chironomid larvae, despite the ongoing grazing of algae by the larvae. More critically, however, benthic GPP increased faster than chlorophyll *a*, indicating that productivity per unit of algal biomass increased as more chironomid larvae were present. Furthermore, *C. islandicus* larvae also grew faster when stocked at higher densities; the increased mass of *C. islandicus* larvae at high densities suggests that the consumer-resource positive feedback is sufficiently strong to generate positive density-dependence of the growth of chironomid larvae. Thus, these experiments show that, at high larval densities, chironomid resource limitation was alleviated by their stimulation of benthic algae. Furthermore, Fig. 1e shows that chlorophyll-specific GPP increased at high consumer biomass; similarly, Fig. 1d shows that *C. islandicus* also reached greater individual mass at high densities. This chironomid-algal positive feedback is one potential mechanism that may explain how the chironomids can reach such extreme densities in the benthos of Lake Mývatn.

Magnitude of consumer-driven nutrient cycling

Alleviation of nutrient limitation by larval activity could play a role in generating the observed positive feedback, especially because internal nutrient cycling is the largest contributor to the nitrogen and phosphorus budgets in Lake Mývatn (Ólafsson 1979) and many other freshwater systems (Vanni 2002). We found that larval excretions

provide concentrated nutrients in the close proximity of benthic algae, which could account for the high quality of larval tubes as a substrate for algae (Hershey et al. 1988). Another possible positive effect of tube building on algal growth rates is the change in physical structure the tubes create. The three-dimensional silk tubes of *C. islandicus* and *T. gracilentus* larvae increase surface area for algal growth, while altering physical characteristics of surface sediments due to the binding properties of larval silk (Ólafsson and Paterson 2004). Furthermore, because the chironomid larvae also consume detritus as 30–50% of their diet (Einarsson et al. 2004, Ingvason et al. 2004), the larvae also mobilize nutrients stored in decaying organic matter and diatom fragments. Thus, the larvae likely increase nutrient availability by both increasing the rate of nutrient cycling and by adding to the pool of biologically available nitrogen and phosphorus through their digestion of detritus.

For illustrative purposes, we can examine the potential significance of nutrient mobilization by larvae relative to other sources in the lake. By multiplying chironomid excretion rates (for nitrogen, 1.05 and 0.38 $\mu\text{g/d}$ for *C. islandicus* and *T. gracilentus*, respectively) by an estimate of larval density from 19 Aug 2014 from one location in the lake (7,500 *C. islandicus* per m^2 and 431,000 *T. gracilentus*), we find that chironomids could move in 8 d the equivalent of the yearly external input of nitrogen ($1.4 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, Ólafsson 1979), which is often the limiting nutrient in the lake (Ólafsson 1979, Einarsson et al. 2004). We can similarly estimate that chironomid larvae could cycle the yearly input of phosphorus ($1.5 \text{ g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) in 30 d. This is based on several simplifying assumptions, including constant excretion and flux rates, as estimated from the excretion assay, that chironomid densities (and size structure) remain relatively constant, and that excretion was the sole source of nutrients in the incubation water samples. Still, these estimates further demonstrate the potential for chironomids to influence whole-ecosystem processes (Hölker et al. 2015). Similarly, prior research has found that chironomids may have a substantial impact on benthic nutrient cycling above densities of 1,000 individuals/ m^2 (Tátrai 1988). Additionally, chironomid behavior may also affect nutrient availability in the benthos, because chironomid bioturbation stimulates NH_4^+ release from sediments (Tátrai 1988, Hölker et al. 2015). In a prior study, another *Chironomus* species liberated NH_4^+ from sediments down to at least 15 cm depth (Lewandowski et al. 2007). In Lake Mývatn, NH_4^+ concentrations are very high in deep sediments, reaching $>1,000 \mu\text{g/L}$ by 20 cm depth (Gíslason et al. 2004). These results also suggest that the rates of nutrient cycling in Lake Mývatn could vary dramatically from year to year, based on larval densities.

Implications for rates of ecosystem productivity

The magnitude of the consumer-resource positive feedback suggests that variability in chironomid abundance could be a strong determinant of primary production in Lake Mývatn. Additionally, the net mutualism

in this consumer-resource system is sufficiently strong as to increase secondary production. It is evident that the positive feedback can generate positive density-dependence in the chironomids, as the *C. islandicus* larvae grew more quickly in mesocosms where they were at high densities. One hypothesis to explain the positive density-dependence in *C. islandicus* is that larvae feed both on and around their tubes, meaning that these chironomids could increase algal availability to neighboring larvae if individuals are sufficiently close. Previous studies of chironomid larval behavior have found evidence of spatial aggregation (Titmus and Badcock 1981, Drake 1983), and we propose that the positive feedback observed in this study may promote behavioral aggregation due to greater local resource availability. Interestingly, the chironomids from treatments with comparatively low larval densities lost mass during the experiment. We hypothesize that all larvae in our mesocosms likely experienced a decrease in their resource availability as a result of establishment of mesocosms. Homogenizing the sediments would have reduced the algal availability in mesocosms, as compared to the original lake sediments. This is because it disrupted the high-quality periphyton resources that were present on sediment surfaces and on larval tubes. Furthermore, larvae could have lost body mass due to metabolic costs incurred as a result of building new tubes and burrows in the mesocosms. For these reasons, we expect that the mass of all larvae would have declined initially upon being relocated to mesocosms. However, larvae in higher density treatments may have regained body mass more quickly due to the higher primary production of these mesocosms.

We also hypothesize that mutualisms between consumers and resources, such as the positive feedback described here, could ultimately translate to population-level effects in these systems. For example, for chironomids at Lake Myvatn, this positive feedback might explain the prolonged period of exponential growth experienced by the chironomids during the upswings in their population fluctuations; the mutualism between the chironomid consumers and the algal resources may be sufficiently strong as to allow for several generations of exponential growth due to a lack of resource limitation. However, it is obvious that at some point, the positive feedback between the chironomid community and the benthic algae breaks down, because the chironomid populations eventually crash. As such, we hypothesize that the relationship between density of chironomid larvae and the rate of benthic algal production may be dependent on other factors not considered in this study, which could lead to a non-linear relationship under different conditions. For example, the proportion of detritus in sediments could be an important modulating factor in the positive feedback (de Mazancourt et al. 1998), as it represents a source of nutrients that are added to the nutrient pool, rather than only recycled within the nutrient pool. Additionally, the stage structure of the

chironomid larvae could be another factor determining the strength of this mutualism. The biomass of larvae in the lake changes substantially throughout the growing season as a result of larvae progressing through stages of development, which could alter the relative rates of consumption and stimulation of benthic algae. Because the chironomids in Lake Mývatn have a finite population size, the linear relationship between chironomid density and chironomid growth must plateau under some circumstances.

Although we have highlighted several reasons to believe that the positive relationship between chironomids and their food resources must break down under different conditions in our study system, it is worthwhile to consider the theoretical case where this effect is uniform across space and time. In the case that all else is held constant, a positive feedback that leads to differential consumer growth rates would be expected to influence population dynamics. Integrating positive feedbacks in consumer-resource systems with the existing theoretical frameworks of consumer-resource population dynamics suggests that systems with consumer-resource mutualisms may have specific population-level characteristics. For example, increased population-level growth rates in the consumer as a result of a mutualism could be considered a type of Allee effect (Allee 1931). Following this framework, a region of positive density-dependence in the consumer should generate a stable equilibrium at a higher density than would occur without the positive feedback (Stephens et al. 1999). In the context of the Lake Mývatn system, this means that the lake benthos might exhibit a tendency to support higher densities of larvae than would occur in the absence of the positive feedback. Furthermore, positive feedbacks within consumer-resource systems often tend to increase the birth rate of the resource (Bianchi et al. 1989). This scenario of variable resource birth rates has been long-studied by theoretical ecologists because it generates the “Paradox of Enrichment,” which occurs when an increase in the per-capita birth rate of a resource destabilizes the population dynamics of a consumer-resource system (Rosenzweig 1971). This well-known result suggests that a positive feedback in a consumer-resource system might predispose the system to instability or cyclic dynamics. Thus, including positive feedbacks into models of consumer-resource systems may have predictable consequences for population dynamics.

Positive feedbacks in consumer-resource interactions

Although chironomid larvae could generate a net positive effect on primary production, these larvae are still consumers of the benthic algae. Thus, the interaction between the larvae and the benthic algae was a combination of facilitation and consumption. Because the larvae stimulated algal growth to a greater extent than they suppressed it through consumption, the larvae and the algal showed a net mutualistic interaction, whereby both taxa had a greater growth rate when the other was

highly abundant. Whereas combinations of species interactions such as competition and predation have been considered simultaneously (e.g., intraguild predation), a similar framework for understanding mutualism in the context of predation is lacking (Vázquez et al. 2015). This study suggests that strong consumer-resource positive feedbacks can affect ecosystem-level properties, such as primary production and producer-to-consumer ratios.

This consumer-resource positive feedback may be important in other systems where grazers are the primary consumers. We investigated here two mechanisms that may contribute to the positive effects of grazers on their resources: nutrient cycling through excretion and ecosystem engineering providing enhanced substrate for growth. However, another contributing factor here might be that benthic bioturbators increase the flux of soluble nutrients out of sediment pore water, making these nutrients available to primary producers (Lewandowski and Hupfer 2005). More generally, there are several other mechanisms whereby grazers could promote the growth of their resources. These mechanisms include increased growth due to a release from shading following grazing, hormone secretions in grazer saliva that induce growth, removal of senescing tissue, release from intraspecific competition, and greater efficiency in resource distribution within the remaining population (McNaughton 1983). Given the myriad mechanisms by which grazers could increase the growth rate of their resources, it would be interesting to look for this positive feedback in other systems, especially investigating whether background nutrient availability influences the strength of the positive feedback.

A recent review of the effect of tube-dwelling invertebrates as ecosystem engineers concluded that it is difficult to determine the importance of tube-dwelling invertebrates at the lake-wide scale (Hölker et al. 2015). However, this study supports the hypothesis that chironomids can be drivers of lake primary production by altering critical feedback loops. This study demonstrates that the positive feedback between tube-dwelling invertebrates and benthic primary producers can significantly affect lake-wide productivity, as benthic GPP can account for upwards of 80% of total aquatic GPP in this system (Jónasson 1979, Thorbergisdóttir et al. 2004). Although the effects of tube-dwelling invertebrates on pelagic primary production have been well studied (Hölker et al. 2015), the critical role these ecosystem engineers play in the benthos has not been documented as thoroughly, even though benthic primary production may be greater than pelagic primary production in shallow lakes (Vadeboncoeur et al. 2008). Finally, this positive feedback may be particularly important in regions where chironomids are used as indicators of water quality, if the chironomid larvae modify their environment by stimulating algal production.

Several previous studies have shown that consumers can have marginal positive effects on resources (McNaughton 1983, Holland and DeAngelis 2010), even if the net effect of consumers is generally negative (Sih

et al. 1985). Despite this observation, positive feedbacks have often been ignored in conceptual models of consumer-resource interactions (Vázquez et al. 2015). However, in this instance, the consumer-resource facilitation was stronger than the effect of consumption; the benthic primary consumer trophic level exerted a net positive effect on their resources. Thus, contrary to the paradigm that aquatic primary consumers are particularly effective at suppressing primary producer biomass (Hairston and Hairston 1993, Shurin et al. 2006), we found that increasing the density of primary consumers could substantially increase benthic NPP and primary producer biomass. These results also highlight the importance of considering the rates of turnover of resources, in addition to standing biomass. Facilitation in consumer-resource interactions, which is often overlooked when net interaction strengths are negative, has the potential to substantially alter traditional consumer-resource dynamics. In the Mývatn system, positive consumer-resource feedbacks can be sufficiently strong as to create a net mutualism between the primary producer and primary consumer trophic levels in the benthos.

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