Ecosystem engineering weakens negative density dependence in an aquatic insect population

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# Abstract

In order to undertand the effects of ecosystem engineering on community dynamics, it is important to characterize density-dependence feedbacks to populations of engineers themselves. In this study, we assessed the sign and magnitude of ecosystem engineering effects on density dependence in midges in the naturally eutrophic Lake Mývatn. The midge larvae reside in the sediment and build silk tubes that provide a substrate for algal growth, thereby elevating benthic primary production. Benthic algae are in turn the primary food source for the midge larvae, setting the stage for the effects of engeering to feed back to thte midges themselves. Using a field mesocosm experiment with a range of larval midge densities, we found a generally positive but highly nonlinear relationship between density and benthic production. Furthermore, adult emergence increased with the primary production per initial midge larvae. By combining these two relationships in a simple model, we found that the positive effect of midges weakened the strength of negative density dependence at low to intermediate larval densities. However, this benefit disappeared at high densities due to the the nonlinearity of midge effects on production. Our results illustrate how ecosystem engineering can alter the strength of density dependence for engineer populations.

*Keywords*: benthic production; facilitation; feedbacks; interpsecific interactions; macroinvertebrates; *T. gracilentus*

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# Introduction

Ecosystem engineering is a class of ecological interactions whereby effects of one population on another are mediated through alterations to the physical environment (Jones, Lawton, and Shachak 1994; Wilby 2002). Like all interspecific interactions, ecosystem engineering has the potential to generate feedbacks among various members of a community (Bertness and Leonard 1997; Largaespada, Guichard, and Archambault 2012; Donadi et al. 2014; Sanders et al. 2014). For example, physical structure provided by coral can ameliorate competition with algae by benefiting grazers that reduce algal abundance (Bozec et al. 2013). As ecosystem engineers are (by definition) the source of engineering effects within an ecosystem, feedbacks between engineering and the engineers themselves are central to the dynamical consequences of engineering for the community as a whole (Hastings et al. 2007; Sanders et al. 2014).

To understand the role of engineering feedbacks for the population dynamics of ecosystem engineers, it is useful to relate those feedbacks to the strength of density dependence (Hastings et al. 2007; Cuddington, Wilson, and Hastings 2009). Using a simple mathematical model, (Cuddington, Wilson, and Hastings 2009) showed that a wide range of dynamical behavior is possible for populations of ecosystem engineers, including stable persistence, extinction, unbounded growth, and alternative states. Two key factors for determining such outcomes are (1) the dependence of engineering effect on population density and (2) the feedback of engineering to density dependence. Despite their theoretical importance, quantitative characterizations of such relationships for natural populations are limited. While previous studies have established the existence of engineering-mediated feedbacks to engineering populations (e.g., Bozec et al. 2013; Donadi et al. 2014; Largaespada, Guichard, and Archambault 2012) they have generally not done so across a range of engineer densities as is required to directly quantify density dependence.

We assessed the effect of ecosystem engineering on the sign and magnitude of density dependence in the midge *Tanytarsus gracilenuts* (Diptera: Chironomidae) in Lake Mývatn, Iceland. The larvae of *T. gracilenuts* dwell in the sediment and build silk tubes that elevate primary production by providing a substrate for algal growth (Herren et al. 2017; Phillips et al. 2019), similar to other aquatic macroinvertbrates (Largaespada, Guichard, and Archambault 2012; Donadi et al. 2014; Hoelker et al. 2015). The larva feed on benthic algae (mainly diatoms), which means that their enhancement of benthic production may benefit their own survival and subsequent reproduction (Ingvason, Ólafsson, and Gardarsson 2004; Einarsson et al. 2002). However, midge consumption may also reduce algal biomass, potentially leading to intraspecific competition and negative density dependence. (Einarsson et al. 2016). Indeed, Mývatn’s *T. gracilenuts* show large fluctuations in abundance that are likely driven by food limiation, although these fluctuations cannot be explained purely in term classical consumer-resource cylces (Ives et al. 2008). Characterizing the nature of density dependence is important for understanding the complex population dynamics of *T. gracilenuts*, making it a good example case for exploring the effects of ecosytem engineering on density dependence.

To evaluate the role of ecosystem engineering on density dependence in *T. gracilenuts*, we conducted a field mesocosm experiment across a range of experimental larval densties. This allowed us to directly quantify (a) the relationship between benthic primary produdction and larval midge density and (b) the relationship between adult emergence rates and primary produdction per larval midge. We then combined these two relationships into a simple model that allowed to isolate the contribution of larval midge effects on primary production to their density dependence.

# Methods

Mývatn is a large (), shallow (mean depth: 2.5m), naturally eutrophic lake in northeastern Iceland (65°40’N 17°00’W) (Einarsson et al. 2004). It is separated into two, ecologically distinct basins (north and south). Our study was conducted in 2017 at three sites (E2, E3, and E5) in the south basin that were selected to represent a range of ecological conditions (Figure [1](#fig:sites)). These sites all have soft substrate that is suitable for *T. gracilentus*, although they can differ in larval densities. In sediment cores taken throughout the summer of 2017, E3 had the highest densities (mean standard error: ), followed by E5 (), and then E2 (). Maximum densities in Mývatn have exceeded (Lindegaard and Jónasson 1979). In the summer of 2017, E2 was subject an expanding mat of filamentous green algae (Cladophorales) that was largely absent from E3 and E5 (J. Phillips; personal observation). Furthermore, E2 was substantially colder during the experiment period than E3 and E5 (Figure [1](#fig:sites)). In contrast, photosynthetically active radiation (PAR) was similar between the sites, due to their similar depths (E2: 2.8m; E3: 3.3m; E5: 2.6m) and similar water clarity throughout the south basin in 2017. Light and temperature data were collected with two loggers (HOBO Pendant, Onset Computer Corporation) deployed on the lake bottom at each site and set to log every 30 minutes. PAR was recorded as visual light intensity (lux) and approximately converted to PAR using a standard scaling factor (Thimijan and Heins 1983).

We conducted our field mesocosm experiment using a design similar to (Phillips et al. 2019). On 28 June 2017, we collected sediment cores from the three study sites using a Kajak corer. For each site, we pooled the sediment from the different cores while keeping the top 5cm (“top”) and next 10cm (“bottom”) separate. We then sieved the sediment through either 125 (top) or 500 (bottom) mesh to remove midge larva. The sediment was left to settle for 4 days in a cool, dark, location. We constructed the mesocosms by stocking the sediment into clear acrylic tubes (33cm height 5cm diameter) sealed from the bottom with foam stoppers. We fist added 10cm of bottom sediment and then 5cm of top sediment, to mimic the layering in the lake. The sediment layer of each mesocosm was wrapped with 4 layers of black plastic to eliminate light from the sides of the mesocosms.

On 3 July, we took sediment cores at E3 and sieved them through 125 to collect Tanytarsini larvae (the vast majority of which were likely *T. gracilentus*). Tanytarsini progress through four instars before emerging as adults. We attempted to select individuals the general size of second instar larvae to maximize the duration of the experiment before emergence. The following day we stocked the mesocosms with four densities of Tanytarsini larvae: 0, 50, 100, 200 per mescosm (0, 25000, 51000, and 102000 ). We then filled the mesocosms with water collected from the southern shore of Mývatn’s south basin and gave the midges 24 h to settle before deploying in the lake. On 5 July, we distributed the mesocosms corresponding to each site onto two racks and then deployed them at their respective sites on the lake bottom. The tops of the mesocosms were left open to allow exchange between the mesocosms and the lake water column.

On 10 and 11 July, we estimated gross primary production (GPP) in the mesocosms by measurnig the change in dissolved oxygen (DO) concentration during sealed incubations (Hall and Hotchkiss 2017). The incubations were conducted in situ at the respective sites to incorporate spatial variation in ambient conditions, such as light and temperature. Each mesocosm was first incubated under ambient light to give an estimate of net ecosystem production (NEP), followed by an incubation under dark conditions produced by wrapping each mesocosm in 4 layers of black plastic to give an estimate of ecosystem respiration (ER). NEP + ER gives an estimate of GPP, assuming that ER is the same during both the light and dark incubations. Half of the mesocosms at each site were incubated on 10 July, while the other half were incubated on 11 July; all of the mesocosms incubated on a given day for a given site were on the same experimental rack and so constituted a “block”. The incubations lasted between approximately 3 and 5 hours, and the tops of the mesocosms were sealed with rubber stoppers for the duration. DO was measured using a handheld probe (ProODO, YSI, Yellow Springs, Ohio, USA), and we gentled stirred the water within each mesocosm to homogenize it before taking the reading. We repeated the incubation procedure on 21 and 23 July. For logistical reasons, we were unable to perform the incubations at the respective sites. Therefore, on 21 July all of the mesocosms were moved to a common location on the southern shore of the south basin (depth 1.7m). The incubations lasted between approximately 3 and 5 hours, while the dark incubations lasted between 4 and 10 hours. While variation in incubation duration was not ideal, the amount of DO in the dark incubations remained above anoxic conditions (minimum DO >10 ). We converted GPP to units of , accounting for incubation duration and water column depth within each mesocosm.

On 23 July, shortly prior to when we expected midges to begin emerging from the mesocosms, we removed the mesocosms from the lake and secured a mesh cover to the top of each to catch adult midges as they emerged. We kept the mesocosms outdoors in mesh tents, using water baths of cold tap water to moderate the temperature of the mesocosms. The water baths had a depth of approximately 18cm, which was sufficient to cover the sediment portion of each mesocosm while leaving the tops exposed to the air to allow emergence. Every 1-3 days for the next 13 days, we collected the emerging adults from the mesocosms. While these were not individually identified, the vast majority appeared to be Tanytarsini. Furthermore, there was a strong association between the number of Tanytarsini larvae stocked in the mesocosms and the number of adults that emerged (Spearman rank correlation of 0.82; $\emph{P}$ < 0.0001; including the zero density treatment).

We quantified the relationship between GPP and initial larval density using a linear mixed model (LMM). The model included initial density (four levels), site (three levels), incubation period (two levels; either 10-11 or 21-23 July), and their two-way interactions as fixed effects. Because we expected the relationship between GPP and initial density to be nonlinear, we also included 2nd and 3rd order polynomial terms for initial density (without any interactions) in the model. We choose a third degree polynomial because this gave the same number of parameters to estimate as would have been the case if each of the four treatments were treated as discrete levels (including the intercept). The polynomial regression had the advantages of (a) allowing us to treat density as a numeric variable and (b) of allowing us to simplify the model by only allowing interactions with the linear density term. We accounted for variation in ambient conditions during the incubations by including linear terms for PAR and temperature estimated for each block at each site. Finally, we included random effects for experimental rack and mesocosm identity to account for blocking and repeated measures, respectively.

We used a binomial generalized linear mixed model (GLMM) to analyze variation in the proportion of the initial number of midge larvae that emerged as adults from each mesocosm (excluding the zero treatment). We included initial density (three levels), site (three levels), and their interaction as fixed effects. We included random effects for experimental rack and mesocosm identity to account for blocking and potential overdispersion, respectively; the latter was equivalent to assuming the residuals followed a logit-normal-binomial distribution. To assess the potential for larval midge effects on GPP to alter the strength of density-dependent emergence, we fit a GLMM similar to the one described above, but with GPP per initial midge larva as the sole fixed effect. We then generated “predicted” values of adult emergence rates under two scenarios (1) using predicted values of GPP as a function of site and density treatment according to the polynomial LMM described above, and (2) using predicted values of GPP fixed across larval density, but including variation across sites, based on the polynomial LMM evaluated at the mean larval density. In scenario (2), GPP per larva declined across the midge treatments purely due to the partitioning of GPP across a greater number of individuals. Scenario (1) included this decline in GPP due to partitioning, but also included any positive or negative effects of larval density on GPP itself. The difference between scenarios (1) and (2) gave a measure of the effect of larval density on the strength of density dependence as mediated through midge effects on GPP.

Statistical analyses were conducted in R 4.0.0, using the “lme4” package to fit the LMM and GLMMs. We calculated $\emph{P}$-values with $\emph{F}$-tests using the Kenward-Roger correction for the LMM (“Anova” function in the“car” package) and with parametric-bootstrapped likelihood-ratio tests (LRTs) based on 2000 simulations for the GLMMs (“simulate” function in the native “stats” package). We used both Type III and Type II tests, to balance concerns with inflated Type-I errors that can occur when dropping terms with the poor statistical inference than can come from overparameterized models.

# Results

The 1st, 2nd, and 3rd degree terms associated with midge larval density were all statistically significant (Table [1](#tab:gpp)), indicating a nonlinear relationship between GPP and larval density. This relationship was generally positive, although it saturated and was possibly negative at the highest densities (Figure [2](#fig:gpp)). On day 7 of the experiment, all three sites had similar GPP-midge relationships and overall levels of GPP. However, there were statistically significant day site, day density, and site density interactions that manifested as a differences between the sites on day 20. In particular, the GPP-midge relationship was weaker on day 20 than on day 7 for sites E2 and E5, while the midge effect at E3 remained largely similar. The sites also diverged in overall GPP through time, with E3 and E5 higher on day 20 than on day 7, while E2 was lower. These relationships corrected for the significantly positive effect of ambient temperature during the measurement incubations. Therefore, the temporal patterns likely reflect real divergences between the productivity of the mesocosms at the three sites through time, rather than transient differences in ambient environmental conditions during the measurements.

The emergence rates of adults declined with initial larval density (Table [2](#tab:adult)), indicating negative density dependence. Neither the main effect of site nor its interaction with density were statistically significant. Emergence rates increased with the GPP per initial larva (LRT: =29.8; $\emph{P}$ < 0.001; Figure [3](#fig:adults)), which is consistent with the hypothesis that negative density dependence is related in part to food limitation. Accordingly, the positive effect of larval density on GPP reduced the strength of negative density dependence across the range of densities used in the experiment (Figure [4](#fig:feed)). The positive effect of midges on their own emergence was maximized at intermediate densities, which corresponds to where the effect of larval density on GPP was maximized (Figure [2](#fig:gpp)). Above this density, the midge effect on GPP plateaued and perhaps even became slightly negative. Therefore, at the highest densities emergence rates converged on what they would be in the absence of midge effects on GPP. There was modest variation in the midge effect on density dependence among the three sites, with the effect being greatest at E3. This reflects the fact that the positive midge effect on GPP declined through time at sites E2 and E5, while at E3 it remained largely consistent.

# Discussion

Our field mesocosm experiment shows how ecosystem engineering can weaken negative density dependence for the population of engineers. We found that *T. gracilentus* larvae in Mývatn have large positive effects on benthic primary production, which previous studies have shown are driven at least in part by physical structure provided by the tubes in which the larvae reside (Hoelker et al. 2015; Phillips et al. 2019). Because *T. gracilentus* larvae feed on benthic diatoms (Ingvason, Ólafsson, and Gardarsson 2004), simulation of benthic production increased the amount of production per individual, which in turn weakened negative density-dependence arising from food limitation.

While the effect off midges on benthic production was generally positive in our experiment, this effect was nonlinear and plateaued between 60,000 and 90,000 individuals . Consequently, the midge-mediated weakening of density dependence was maximized at intermediate densities. Given the suppression of algal biomass through grazing (Einarsson et al. 2016), it is likely that the effect of midges on production becomes negative at the highest densites observed in the lake (>200,000 ). This suggests that while midges weaken negative density dependence at moderate densities, they may enhance it at the highest densities. The nonlinearity of ecosytem engineer effects has previously been identified as an important factor in governing the effects of engineering on community dynamics (Bozec et al. 2013). Despite weakening densitity dependence at low to moderate densities, midge engineering did not lead to positive densitiy dependence (i.e., allee effects; Courchamp, Clutton-Brock, and Grenfell 1999). This has important implications for their population dynamics, as positive density dependence could lead to run-away or overcompensatory growth (Turchin 2003; Cuddington, Wilson, and Hastings 2009).

The midge effect on benthic producivity across the three sites was similar at the beginning of the experiment, but diverged through time even after accounting for variation in ambient conditions during the productivity measurements. This suggests that there was a legacy of local conditions that affected the response of benthic producers to midge engineering. While our experiment was not directly able to test for such legacies, a plausible candidate is temperature, which was consistently lowest at the site with the weakest response to midges. Various studies have identified the role of environmental variation in mediating the strength and sign of ecosystem engineering (Wright et al. 2006; Lathlean and McQuaid 2017). Enduring legacies of environemtnal mediation are particularly important, as they may serve to decouple the dynamics of the engineers and their community-wide effects (Cuddington 2011). Such decoupling may in tern alter the nature of density-dependent feedbacks in systems with ecosystem engineering (Cuddington, Wilson, and Hastings 2009).

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