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Shifts in the partitioning of benthic and pelagic primary production within and across summers in Lake Mývatn, Iceland

Amanda R. McCormick [ID], Joseph S. Phillips [ID],[§] Jamieson C. Botsch [ID], and Anthony R. Ives [ID]

Department of Integrative Biology, University of Wisconsin–Madison, Madison, WI, USA

ABSTRACT

The relative contributions of benthic and pelagic primary production affect ecosystem function, but studies documenting natural variation in the partitioning of production (i.e., autotrophic structure) are uncommon. This study examines autotrophic structure of shallow Lake Mývatn over 7 summers (2012–2018). We used routine measurements of benthic gross primary production (GPP), pelagic chlorophyll *a* concentrations, and pelagic production to estimate benthic and pelagic maximum productivity (P_{max}) across summers. With these parameters and corresponding incident light and water clarity data, we estimated in situ benthic and pelagic GPP. Our results demonstrated substantial variation in Mývatn's autotrophic structure within and across summers. Benthic GPP often exceeded pelagic GPP. However, periods of increased phytoplankton abundance were associated with increased light attenuation and, consequently, declines in benthic GPP. These effects were strongest in 3 summers with dense cyanobacteria blooms, in which the benthic fraction of total production declined from >95% to <20%. Reduced light levels over a 2-week period were associated with low benthic P_{max}, implying that past shading by phytoplankton may decrease the photosynthetic potential of benthic producers. Moreover, variation in estimated benthic P_{max} values can affect the point at which autotrophic structure shifts toward pelagic-dominated conditions. Overall, our study demonstrates that the balance between benthic and pelagic production can vary greatly at intra- and interannual scales because of changes in the photosynthetic capacity of both pelagic and benthic primary producers. Understanding natural variation in lake autotrophic structure may inform how benthic and pelagic production respond to ongoing and future environmental changes.

Introduction

Benthic and pelagic primary production comprise whole-lake production, and the relative contribution of these components, or autotrophic structure (Higgins et al. 2014), plays a central role in ecosystem function. Autotrophic structure is influenced by interactions among lake bathymetry, morphology, water clarity, and nutrient concentrations (Sand-Jensen and Borum 1991, Vadeboncoeur et al. 2008). Some static lake characteristics (e.g., basin shape) can create patterns in the partitioning of primary production in comparisons among lakes. For example, deep, steep-sided lakes with little illuminated benthic habitat are commonly pelagic dominated while shallow lakes with expansive, flat littoral surfaces are more likely to support high benthic production (Wetzel 2001, Vadeboncoeur et al. 2008). However, a lake's autotrophic structure is not necessarily fixed through time because variation in physicochemical and biological factors (e.g., water

clarity, nutrient concentration) can alter the relative contributions of benthic and pelagic primary producers to total production. In particular, shallow lakes may experience dramatic shifts in autotrophic structure alternating between "clear" and "turbid" states, dominated by benthic or pelagic production, respectively (Scheffer et al. 1993, Genkai-Kato et al. 2012).

The competitive relationship between pelagic (phytoplankton) and benthic (periphyton, epipelon, macrophytes) primary producers affects the partitioning of production within a lake (Jäger and Diehl 2014). Specifically, epipelic algae living on the sediment surface can limit phytoplankton production by reducing nutrient flux to the water column (Carlton and Wetzel 1988, Hansson 1988). Phytoplankton increase the attenuation of light through the water column, thereby reducing benthic light availability (Sand-Jensen and Borum 1991, Hansson 1992). Thus, stimulation of pelagic primary producers and the associated shading can

immediately and directly decrease benthic primary production and the contribution of benthic algae to whole-lake production (Vadeboncoeur et al. 2003, 2008).

In addition to in situ light availability, realized rates of benthic primary production are also affected by parameters governing the relationship between photosynthesis and irradiance (i.e., the P-I curve). Photosynthetic rates increase linearly with light availability at low irradiance levels and generally plateau at a maximum rate of production (P_{max}) when light intensity is saturating (Jassby and Platt 1976). P_{max} can be considered the photosynthetic potential of an algal community, and variation in benthic P_{max} can affect lake autotrophic structure (Vadeboncoeur et al. 2008, Brothers et al. 2016). For example, when modeling autotrophic structure across a eutrophication gradient, Vadeboncoeur et al. (2008) found that benthic production was <50% of total production when benthic P_{max} was low, whereas benthic production typically dominated when benthic P_{max} was intermediate or high, even in mesotrophic conditions. Benthic P_{max} may especially influence the benthic contribution to total production in clear shallow lakes in which saturated light levels likely occur over a larger benthic area and for longer periods of time than in deeper lakes.

While the reduction in benthic light availability is a direct and well-documented negative effect of phytoplankton on benthic primary production (Hansson 1992, Vadeboncoeur et al. 2001, 2003), it is less clear whether prolonged shading affects benthic P_{max}. Reduction of benthic P_{max} would imply that processes determined by phytoplankton (e.g., extended periods of shading) alter the photosynthetic potential of benthic primary producers. These effects of phytoplankton are plausible; several limnological studies describe associations between ambient light conditions and benthic P-I parameters (Vadeboncoeur and Lodge 2000, Liboriussen and Jeppesen 2003, Brothers et al. 2016, Devlin et al. 2016). For example, epipelic and epilithic P_{max} rates may decline with increasing depth (Jónsson 1992, Vadeboncoeur and Lodge 2000), and high periphyton P_{max} are associated with clear-water systems (Brothers et al. 2016). The link between benthic P_{max} and the ambient light environment may be partly mediated by light's effect on algal biomass. Previous studies have shown that prolonged experimental shading can reduce periphyton chlorophyll a (Chl-a) concentration (Hansson 1988, Steinman et al. 1990), which is often considered a biomass proxy. Other studies have documented positive relationships between benthic P_{max} and benthic primary producer biomass (Boston and Hill 1991, Dodds et al. 1999). Together, these results suggest that

if prolonged shifts in the benthic light environment have the potential to decrease algal biomass, they may thereby affect P_{max}. This process suggests that prolonged phytoplankton shading may indirectly affect benthic productivity by influencing benthic P_{max}, with this indirect effect occurring on a delayed time scale. Thus, a shift to a pelagic-dominated autotrophic structure could affect the relative contribution of benthic algae to total production by influencing their photosynthetic potential in addition to directly reducing in situ benthic light availability.

While lake autotrophic structure may exhibit temporal variation, capturing these dynamics is often challenging. Whole-lake and mesocosm experiments (Björk-Ramberg and Ånell 1985, Vadeboncoeur et al. 2001, Vasconcelos et al. 2016), observational studies (Liboriussen and Jeppesen 2003, Althouse et al. 2014), and theoretical models (Vadeboncoeur et al. 2008, Genkai-Kato et al. 2012, Higgins et al. 2014) are useful for investigating factors and mechanisms that shift the partitioning of benthic and pelagic production. However, contemporaneous measurements of benthic and pelagic primary production through time under natural conditions are relatively rare (Liboriussen and Jeppesen 2003, Althouse et al. 2014). Ongoing consequences of global change (e.g., eutrophication, increased dissolved organic carbon loading, invasive species establishment; Smith and Schindler 2009, Havel et al. 2015, Solomon et al. 2015) will likely affect the partitioning of benthic and pelagic primary production (Vadeboncoeur et al. 2001, Karlsson et al. 2009, Higgins et al. 2014). Understanding natural temporal variation in autotrophic structure could provide insight into how these ongoing stressors will affect lakes in the future (Althouse et al. 2014).

Lake Mývatn is well suited for examining temporal variability in the partitioning of benthic and pelagic production and the ecological consequences of shifting autotrophic structure. Mývatn's shallowness supports high primary production on the surface of its nutrient-rich sediments, with epipelic algae generally contributing a majority of total production (Ólafsson 1979a, Einarsson et al. 2004). However, Mývatn is also naturally eutrophic, with high external phosphorus loading from nutrient-rich groundwater springs (Ólafsson 1979a) and potentially high internal loading of nutrients from the sediment (Gíslason et al. 2004). The resulting high nutrient availability in the pelagic habitat implies the potential for phytoplankton dominance (Jäger and Diehl 2014). Phytoplankton, especially cyanobacteria, blooms occur with variable timing and intensity in Mývatn. In some years, cyanobacteria blooms spread throughout much of the lake while in

other years the lake maintains a reasonably clear-water state (Einarsson et al. 2004). Phillips (2020) modeled whole-ecosystem metabolism (integrating both pelagic and benthic habitats) over multiple years in Mývatn and showed that cyanobacterial blooms may be strongly linked to variation in the lake's photosynthetic potential. Thus, Mývatn presents an ideal opportunity to examine temporal dynamics in the balance between benthic and pelagic production.

In this study we analyzed monitoring data associated with benthic and pelagic primary producers in Mývatn, including regular measurements of benthic gross primary production (GPP) and phytoplankton biomass (Chl-*a*), for 7 summers (2012–2018). Using these monitoring data, as well as supplemental measurements to characterize pelagic primary production, we examined temporal trends in benthic and pelagic P_{max} (i.e., the maximum rate of primary production for either habitat). We combined the estimates of P_{max} with incident irradiance and light attenuation data to estimate in situ benthic and pelagic GPP. Our primary objectives were to (1) determine whether algal biomass and previous light conditions contribute to variation in benthic P_{max}, (2) examine competitive effects of phytoplankton on benthic production through shading, and (3) investigate how variation in benthic P_{max} may influence the overall effect that a shift in autotrophic structure has on total (i.e., summed benthic and pelagic) GPP.

Methods

Study system

Mývatn is a large (37 km^2), naturally eutrophic, shallow lake located in northeast Iceland (65°35′N; 17°00′W). The main basin (28.2 km^2), which includes our study site, has a mean depth of 2.3 m and maximum depth of 4.2 m (Jónasson 1979). Ice cover duration has historically averaged 189 days per year, from October to May (Rist 1979). During ice-free periods, the main basin does not stratify, with wind action helping to maintain mixing during summer (Ólafsson 1979b). Water temperatures in Mývatn respond to fluctuations in air temperature (Ólafsson 1979b; Supplemental Fig. S1). During this study's monitoring period, average daily water temperatures generally ranged from 8 to 17 °C (mean = 12.2 °C), although summer water temperatures may drop to nearly 5 °C (Supplemental Fig. S1). Windstorms can transiently affect lake water level by pushing water toward the leeward shore, and gales can cause water level fluctuations of up to 40 cm in the main basin (Rist 1979). The lake's water renewal time is 27 days (Ólafsson 1979b), and the River Laxá forms its major outlet. Inputs to the lake include nutrient-rich springs along the eastern shore and the Grænilækur River draining the spring-fed Lake Grænavatn; together these contribute 1.5, 1.4, and 340 g m^{-2} y^{-1} of nitrogen (N), phosphorus (P), and silicon (Si), respectively, to Mývatn (Ólafsson 1979a). Internal loading is potentially high, with estimated diffusive nutrient fluxes from the sediment of 0.13 and 1.89 g m^{-2} y^{-1} for PO$_4^{3-}$-P and NH$_4^+$-N, respectively (Gíslason et al. 2004). However, actual nutrient flux rates from the sediment to the overlying water column do not necessarily reflect diffusive rates within the sediment. During much of the summer, net nutrient flux is from the overlying water toward the benthos, which suggests the role of epipelic primary production in determining nutrient flux (Thorbergsdóttir and Gíslason 2004).

Benthic primary production substantially contributes to Mývatn's whole-lake production (Einarsson et al. 2004). Much of the lake has a soft substrate, and epipelic diatoms (especially Fragilariaceae) are major contributors to benthic primary production. Mats of filamentous green algae (*Cladophora glomerata* and *Aegagropila linnaei*) can also cover substantial portions of the main basin, although their spatial extent is highly variable on a decadal time scale (Einarsson et al. 2004). Macrophytes are uncommon in Mývatn's main basin, but they are abundant in the north basin (dominant species: *Potamogeton* spp. and *Myriophyllum spicatum*) and the eastern part of the lake near the groundwater springs (dominant species: *Ranunculus trichophyllus* and *Myriophyllum alterniflorum*; Einarsson et al. 2004). While the lake's shallowness allows high benthic light availability, intermittent phytoplankton blooms and wind-driven sediment resuspension reduce water column transmissivity and create a variable light environment for benthic algae (Jónasson and Adalsteinsson 1979, Phillips et al. 2019). Cyanobacteria blooms are a natural occurrence in Mývatn, and the water column's low N: P ratios are favorable for N-fixing taxa such as *Dolichospermum* (Ólafsson 1979a). Annual *Dolichospermum* blooms typically develop in Mývatn's smaller northern basin (8.5 km^2), which is connected to the main basin by a narrow passage. The spatial extent and intensity with which the blooms spread throughout the main basin are variable across years (Einarsson et al. 2004). In addition to cyanobacteria, other phytoplankton include chlorophytes (*Oocystis*, *Sphaerocystis*, *Pediastrum*), diatoms (Fragilariaceae), and chrysophytes (*Uroglena*, *Dinobryon*), with the abundances of these taxa often varying spatially across the lake (Jónasson and Adalsteinsson 1979, Dickman et al. 1993, Bartrons et al. 2015).

Monitoring site

Our study incorporates data collected from a site located near the center of Mývatn's main basin (depth 3.3 m) that has been routinely monitored from 2012 to 2018 from late May to late August, with (mean [standard deviation]) 9 (3) d between successive sample events. Profiles of photosynthetically active radiation (PAR in photons; µmol m^{-2} s^{-1}; Li-192 Quantum Underwater Sensor, Li-COR, Lincoln, NE, USA) were recorded at 0.5 m intervals through the water column. For each sampling event, we determined a light attenuation coefficient (k_D) by regressing log-transformed PAR against water column depth. We estimated PAR levels just below the water surface (PAR$_{water\ surface}$) using the empirical relationship between our routine PAR profiles and incident light (see Supplemental Materials for details). A sonde (Hydrolab DS5X, Hach, Loveland, CO, USA) at the monitoring site recorded phycocyanin levels (a cyanobacteria pigment), turbidity, and other physicochemical data.

On each sample event, we also measured pelagic and benthic Chl-a concentrations. Water (3–5 analytical replicates) was collected from a single homogenized, integrated water column sample and filtered onto glass-fiber filters (Whatman GF/F) for subsequent analysis of pelagic Chl-a. We collected 5 replicate sediment cores to determine benthic Chl-a concentrations and sediment water content. Minor modifications were made during the study regarding the depth of sediment collected for these analyses; in 2014, 2015, and the first 3 sampling dates of 2016, the top 2 cm layer of sediment was used, but the top 0.75 cm layer was used otherwise. For our statistical analysis, we considered the potential effects of this methodological difference (discussed in methods). The filtered water and sediment samples were frozen, and Chl-a was then extracted in 100% methanol for 24 h in the dark and read on a fluorometer (AquaFluor, Turner Designs, San Jose, CA, USA), using acidification to correct for phaeophytin concentrations. We accounted for water content of the sediment by dividing benthic Chl-a concentrations by the dry weight proportion of the sediment sample. Benthic Chl-a and pelagic Chl-a data were aggregated by date for subsequent analysis.

Characterizing benthic P-I curve parameters

Estimating in situ benthic and pelagic primary production was a central objective of this study, requiring information about the parameters underlying P-I curves for primary producers from these respective habitats. Benthic production was routinely measured during the study, with these measurements spanning a range of ambient light levels driven by the conditions on each sampling day. We used these routine production measurements to accomplish 2 goals: (1) determine a light level corresponding to the average half-saturation point of benthic primary production, and (2) estimate the P_{max} associated with each production measurement based on this parameter. A tabular overview of the measured values and parameters used to characterize benthic primary production complements the explanation that follows (Table 1).

On routine sample dates, we measured benthic GPP, which we refer to as the "observed" GPP (GPP$_{obs}$). We collected intact sediment cores and incubated them 0.5 m below the water surface under ambient light (n = 5 or 6) or fully dark (n = 5 or 4) conditions to respectively measure net ecosystem production (NEP) and ecosystem respiration (ER) based on the change in dissolved oxygen (DO) concentrations (see Supplemental Material for details). Under the assumption that ER is equal in light and dark, we calculated GPP$_{obs}$ for each sample date as the summed magnitudes of the mean NEP and mean ER rates.

Table 1. Definitions for measured values and parameters used to characterize benthic and pelagic primary production.

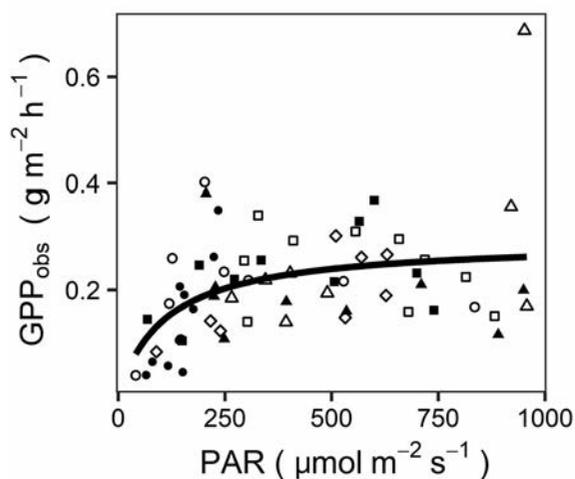| Term	Units	Description	Method for obtaining
Benthic primary production			
GPP$_{obs}$ (O$_2$)	g m^{-2} h^{-1}	Observed GPP from routine incubations	Measured in routine incubations occurring 0.5 m below the water surface
$I_{incubation}$	µmol m^{-2} s^{-1}	Light level corresponding to a GPP$_{obs}$ measurement	Measured during each routine incubation at the 0.5 m incubation depth
$K_{benthic}$	µmol m^{-2} s^{-1}	Light level at which benthic production is half the maximum rate	Estimated parameter from fitting P-I curve to $I_{incubation}$ and GPP$_{obs}$ data (Fig. 1)
P_{max} (O$_2$)	g m^{-2} h^{-1}	Maximum benthic photosynthetic rate	Calculated for each sample date based on $K_{benthic}$ and GPP$_{obs}$ and $I_{incubation}$ for each sample date
Pelagic primary production			
$K_{pelagic}$	µmol m^{-2} s^{-1}	Light level at which pelagic production is half the maximum rate	Estimated parameter from fitting P-I curve to light gradient incubation data (Fig. 2)
s	g O$_2$ m^{-2} h^{-1} (µg Chl-a L^{-1})$^{-1}$	Scaling factor translating pelagic Chl-a concentrations to P_{max}	Estimated parameter from fitting P-I curve to light gradient incubation data (Fig. 2)
P_{max} (O$_2$)	g m^{-2} h^{-1}	Maximum pelagic photosynthetic rate	Calculated for each routine pelagic Chl-a concentration based on scaling factor, s

GPP$_{obs}$ was measured on days spanning a range of ambient light conditions. Using the data from all samples, we fit a Michaelis–Menten type equation:

$$GPP = \overline{P_{max}} \cdot I/(K + I), \qquad (1)$$

(sensu Jónsson 1992, Daniels et al. 2015), in which I is the in situ light level, $\overline{P_{max}}$ is the maximum rate of primary production (with the overbar to distinguish it from the date-specific P_{max} used below), and K is the light level at which GPP = ½ $\overline{P_{max}}$ (i.e., the half-saturation irradiance). We fit equation 1 to GPP$_{obs}$ and the PAR level recorded at 0.5 m during each incubation using nonlinear least squares with the *nls()* function in R (Fig. 1). This produced an estimate of K for benthic primary production ($K_{benthic} = 111$ μmol m^{-2} s^{-1}), which is comparable to half-saturation irradiance levels for epipelon in other shallow lakes (Daniels et al. 2015). We assumed $K_{benthic}$ to be fixed through time. In our case, it was not possible to determine temporal variation in this parameter because we did not conduct incubations across a gradient of light for each sample date.

Using $K_{benthic}$, we estimated a separate P_{max} value for each sample date based on the measured GPP$_{obs}$ and light conditions during the incubation ($I_{incubation}$), such that P_{max} was allowed to vary through the study's duration. We estimated P_{max} for each sample date by substituting P_{max} for $\overline{P_{max}}$ in equation (1) and

rearranging to yield the expression

$$P_{max} = GPP_{obs} \cdot (I_{incubation} + K_{benthic})/I_{incubation}. \qquad (2)$$
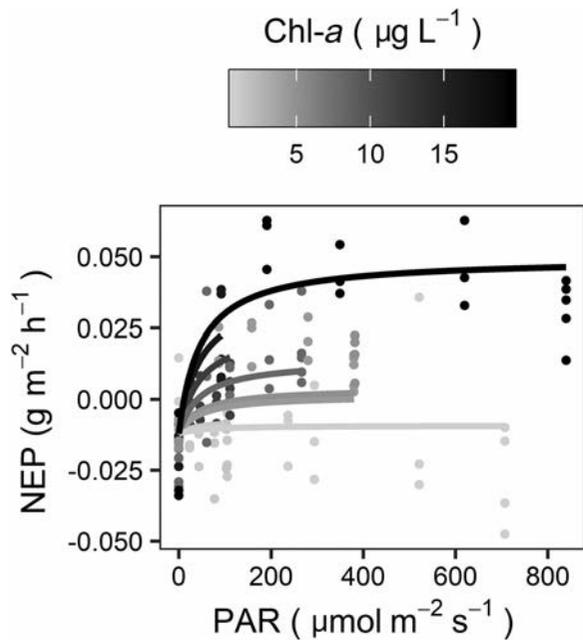
Because the incubations were performed only 0.5 m below the water's surface, many GPP$_{obs}$ values should approximate maximum benthic photosynthetic rates under light-saturating conditions. However, incubations sometimes occurred on days with overcast conditions that likely did not provide adequate light for the onset of light saturation (Fig. 1), and our approach allowed us to estimate benthic P_{max} rates and subsequently estimate in situ benthic GPP across the study duration, thereby taking advantage of the full temporal extent of the data.

Characterizing pelagic P-I curve parameters

Similar to benthic primary production, estimating in situ pelagic primary production across summers was a central objective of the study. We measured pelagic primary production across a range of light levels to (1) estimate a half-saturation irradiance for pelagic primary producers and (2) determine an empirical relationship between pelagic Chl-*a* concentrations and P_{max}. This information allowed us to translate our routinely measured pelagic Chl-*a* measurements into corresponding pelagic P_{max} rates (Table 1).

In summer 2018, we measured pelagic metabolism at 3 sites, with 3 DO incubations per site. Incubations occurred across a range of shading levels from complete darkness to full ambient light (3–5 replicates per shading level; see Supplemental Material for details). We measured Chl-*a* concentrations from replicates receiving full ambient light and used the mean concentration for each site-date combination for subsequent P-I curve fitting.

We fit a single P-I model to pelagic production data from all sites and sample dates. We included the mean Chl-*a* concentration for each site–date combination as a covariate, such that Chl-*a* concentrations were assumed to drive variation in P_{max} across incubations. Assuming that GPP is equal to the summed magnitudes of NEP and ER, we fit a modified equation (1): NEP = $(s \cdot $Chl-$a \cdot$ I$)/(I + K) -$ ER, to our data (Fig. 2). This calculation produced a K value for pelagic primary producers ($K_{pelagic} = 46$ μmol m^{-2} s^{-1}) and allowed P_{max} rates to vary as driven by Chl-*a* concentrations. The parameter s from the fitted model describes the relationship between Chl-*a* (μg L^{-1}) and the P_{max} (O$_2$: g m^{-2} h^{-1}; estimate [standard error] = 0.0032 [0.0003]; $t = 10.06$, df = 120, $p < 0.001$), which we subsequently used to estimate P_{max} corresponding to our

Figure 1. Benthic gross primary production (GPP$_{obs}$ measured as O$_2$) measured routinely from late May to late August for 7 summers of monitoring at our study site. Each point represents a single sample date, with the in situ irradiance level (measured in photons) during the incubation. The line shows the fit of a Michaelis-Menten P-I curve.

Figure 2. The relationship between net pelagic primary production (measured as O_2) and irradiance characterized at 3 sites, with 3 incubations per site in 2018. The line shows a Michaelis-Menten P-I curve fit to the production data, which included pelagic Chl-*a* as a covariate influencing variation in the maximum productivity rate for each incubation. A limited range of PAR (x-axis) occurred on cloudy days.

pelagic Chl-*a* measurements from 2012 to 2018. We investigated the potential for photoinhibition by fitting our data to the model presented in Platt et al. (1980) and found little evidence for photoinhibition.

For our study, we assumed that $K_{pelagic}$ and the relationship between pelagic P_{max} and Chl-*a* are fixed across multiple years. However, temporal variation in taxonomic composition and abiotic conditions (e.g., nutrients, light) may affect the accuracy of extending the estimated $K_{pelagic}$ parameter because these factors can influence photosynthetic potential and efficiency (Richardson et al. 1983, Litchman and Klausmeier 2008, Edwards et al. 2015). Additionally, our approach relies on Chl-*a* concentrations to explain pelagic P_{max} rates, but taxonomic variations in pigment composition may affect interpretation of the relationship between Chl-*a* concentrations and P_{max} rates. Nonetheless, previous studies have approximated pelagic P_{max} from phytoplankton biomass (Guildford et al. 1994, Vadeboncoeur et al. 2008). Because *Dolichospermum* was the dominant phytoplankton group when we conducted our metabolism measurements in 2018, our estimates of pelagic primary production may be affected when other algal divisions (e.g., chlorophytes) were dominant.

Estimating in situ benthic and pelagic production

We estimated in situ benthic and pelagic primary production for dates with corresponding benthic GPP_{obs} and pelagic Chl-*a* data. We calculated in situ light (I_z) at a given depth, z, from the light attenuation coefficient (k_D) and light at the water's surface (I_0; i.e., PAR $_{water\ surface}$; Supplemental Material) as $I_z = I_0 e^{-k_D \cdot z}$. To factor out day-to-day differences in irradiance, we calculated hourly surface water PAR levels across a 1-week window (including the sample date, the 3 preceding days, and the 3 following days). For benthic production, we estimated in situ hourly GPP (across a 24 h period comprising the mean hourly light levels for the corresponding 1-week window) based on equation (1): $GPP = P_{max} \cdot I_{3.3}/(K_{benthic} + I_{3.3})$, where $I_{3.3}$ is the estimated irradiance at 3.3 m. To estimate hourly in situ pelagic GPP throughout the water column, we integrated equation (1) through the maximum depth at which phytoplankton were assumed to occur (z_{chl}; see below): $\int_0^{z_{chl}} P_{max} \cdot I_0 \cdot e^{-k_D \cdot z}/(K_{pelagic} + I_0 \cdot e^{-k_D \cdot z})\, dz$. We then summed hourly benthic and pelagic GPP to estimate daily in situ GPP for each habitat. Photosynthetic parameters for benthic and pelagic algal communities likely vary spatially across Mývatn because of depth differences (Devlin et al. 2016) or heterogeneous phytoplankton distribution (Bartrons et al. 2015). Thus, we present in situ GPP rates for a column of the lake extending above our 3.3 m-deep sampling site rather than extrapolating our estimates across varying depths of the lake. We present our estimated P_{max} and in situ GPP rates in units of carbon (C) by assuming a photosynthetic quotient of 1, corresponding to a 1:1 molar ratio for oxygen (O_2) and C (Thorbergsdóttir and Gíslason 2004). To present the partitioning of primary production into benthic and pelagic components, we calculated the benthic fraction of total primary production at our study site by dividing daily benthic GPP by the sum of daily benthic and pelagic GPP (Vadeboncoeur et al. 2008, Higgins et al. 2014).

Because routine pelagic Chl-*a* measurements were obtained from integrated water column samples, we lack quantitative information about the vertical distribution of phytoplankton. While phytoplankton distribution through the water column may be heterogeneous because of variation in the physical environment (e.g., vertical gradients in temperature, nutrients, light), the distribution of Chl-*a* into distinct layers is unlikely for well-mixed lakes (Klausmeier and Litchman 2001, Longhi and Beisner 2009). We assumed a uniform distribution of Chl-*a* throughout Mývatn's water column, such that $z_{chl} = 3.3$ m (see earlier). The

pelagic production decrease with depth was therefore assumed to be due only to light attenuation through the water column (because our P-I equation does not incorporate photoinhibition). However, previous measurements of pelagic production at Mývatn have shown that in certain conditions (e.g., sunny days) photosynthetic rates can increase to the depth that provides optimal light conditions (Jónasson and Adalsteinsson 1979). During thick blooms at Mývatn, cyanobacteria can concentrate within the upper layer of the water column and subsequently affect the vertical limit for phytoplankton production (Jónasson and Adalsteinsson 1979). Thus, we also reported temporal comparisons of benthic and pelagic P_{max} and estimated in situ benthic and pelagic GPP under the assumption that phytoplankton Chl-*a* is evenly distributed through the euphotic zone (Supplemental Fig. S2, S3), whose lower boundary occurs where the in situ light level is 1% of surface PAR (Reynolds 2006). The euphotic zone typically exceeded our study site depth of 3.3 m, but 2014 and 2015 had minimum euphotic zone depths of 1.92 and 2.02 m, respectively (Supplemental Fig. S4).

Our estimates of in situ production were based on quantities with associated uncertainties, which we propagated when calculating error for in situ GPP (Taylor 1982). Standard deviation for estimated hourly in situ benthic GPP was propagated based on error in the GPP$_{obs}$ measurement from the field incubations and error in estimating $K_{benthic}$. For hourly in situ pelagic GPP, standard deviation was propagated based on error in estimating $K_{pelagic}$ and *s* (the coefficient describing the relationship between P_{max} and Chl-*a*), as well as the fact that variance in the estimates of these parameters were correlated (i.e., they were obtained from the same model fit to our data shown in Fig. 2). Errors associated with hourly benthic and pelagic GPP were propagated when obtaining standard deviation for the estimated daily GPP rates for each respective habitat. Lastly, the errors associated with daily benthic and pelagic GPP rates were propagated when calculating the standard deviation in the benthic fraction of total production.

In addition to investigating temporal trends in benthic and pelagic production estimated across 7 summers, we visually explored how variation in phytoplankton biomass and benthic P_{max} can influence autotrophic structure (sensu figure 4 in Vadeboncoeur et al. 2008). We qualitatively compared how partitioned GPP (i.e., either benthic or pelagic GPP), the combined benthic and pelagic (i.e., total) GPP, and the benthic fraction of total GPP varied across our observed range of pelagic Chl-*a* concentrations (0.48–64.42 µg L^{-1}) for the range of our benthic P_{max} values (C: 29–288 mg m^{-2} h^{-1}). We present 2 visualizations: one focuses on 5 benthic

P_{max} values (minimum, first quartile, median, third quartile, maximum) to summarize the variation in our data, and the other encompasses continuous benthic P_{max} values constrained by our observations. In our dataset, light attenuation coefficients were strongly related to pelagic Chl-*a* concentrations; however, because we could not conduct our sampling in windy conditions (for safety reasons), our data may not fully capture how sediment resuspension affects water clarity in Mývatn. We empirically modeled the relationship between k_D (m^{-1}) and pelagic Chl-*a* (µg L^{-1}; Supplemental Fig. S5), which allowed us to estimate light attenuation coefficients for the hypothetical combinations of pelagic Chl-*a* and benthic P_{max}. We standardized the incident light conditions for our visualization using average diel irradiance levels (Supplemental Fig. S6), which consisted of mean hourly surface water light levels across days contained within the 7 summer sampling periods.

Time series analysis

We investigated biotic and abiotic factors contributing to variation in our measured benthic P_{max} rates. In our analysis, we included benthic P_{max} as the response variable and 2 predictor variables: benthic Chl-*a* standardized to percent sediment dry weight and the cumulative benthic light availability over the 2 weeks preceding the incubation. We included benthic Chl-*a* based on the hypothesis that benthic algal biomass would positively affect maximum rates of primary production. We included a categorical covariate to account for the 2 different sampling depths (0.75 or 2 cm) for collecting sediment samples (see methods). Accounting for this methodological difference did not change the interpretation of the analysis, so we omitted inclusion of the categorical variable when presenting the results.

We included the 2-week cumulative light availability in our analysis under the rationale that the light environment experienced by benthic algae could potentially influence their maximum photosynthetic capacity. To calculate cumulative benthic light availability, we summed hourly benthic light levels over the 2-week period preceding each sampling date, which required intervening light attenuation coefficients that we estimated from turbidity data (see Supplemental Materials for details). This analysis investigated a mechanism (the recently experienced light environment) that could explain variation in benthic P_{max}. We performed complementary analyses to investigate the effects of biotic conditions (phytoplankton abundance) on the same variation in benthic P_{max}. Specifically, in 2 separate analyses we analyzed whether either lagged pelagic

Chl-*a* concentrations or lagged phycocyanin levels affect benthic P_{max} (Supplemental Material).

To statistically describe the effect of a specific predictor variable on benthic P_{max}, we compared models with and without the given predictor variable using a likelihood-ratio test (LRT). Models accounted for temporal autocorrelation within years and were fit as linear models using generalized least squares with the *gls()* function within the *nlme* package (Pinheiro et al. 2019) in R. Before the analyses, we first log-transformed benthic P_{max} and benthic Chl-*a* because they had skewed distributions and then *z*-transformed all variables across years by subtracting the respective variable's mean from each observation and dividing by that variable's standard deviation. All analyses were performed in R 3.6.1 (R Core Team 2019).

Results

Ambient conditions across years

The water column clarity at the study site was variable, with observed light attenuation coefficients ranging from 0.18 to 2.39 m^{-1}. Summers generally began with relatively low light attenuation coefficients (mean k_D was 0.45 m^{-1} across sample dates in May and June), but k_D increased in the latter parts of some summers (Fig. 3). Pelagic Chl-*a* concentrations were also variable (Fig. 3). Pelagic Chl-*a* markedly increased throughout some summers, but this temporal trend was inconsistent among years. Increased pelagic Chl-*a* concentrations were associated with low water clarity (Fig. 3, Supplemental Fig. S5). Based on water column phycocyanin data and visual observations, the increases in pelagic Chl-*a* concentrations during 2014, 2015, and 2018 can be attributed to cyanobacteria blooms of *Dolichospermum* (Fig. 3).

Benthic and pelagic P$_{max}$ rates

The pelagic P_{max} rates estimated from pelagic Chl-*a* data were generally much lower than benthic P_{max} rates measured using metabolism incubations (Fig. 4, Supplemental Fig. S2). The magnitude of pelagic P_{max} was often <10% of the corresponding benthic P_{max}.
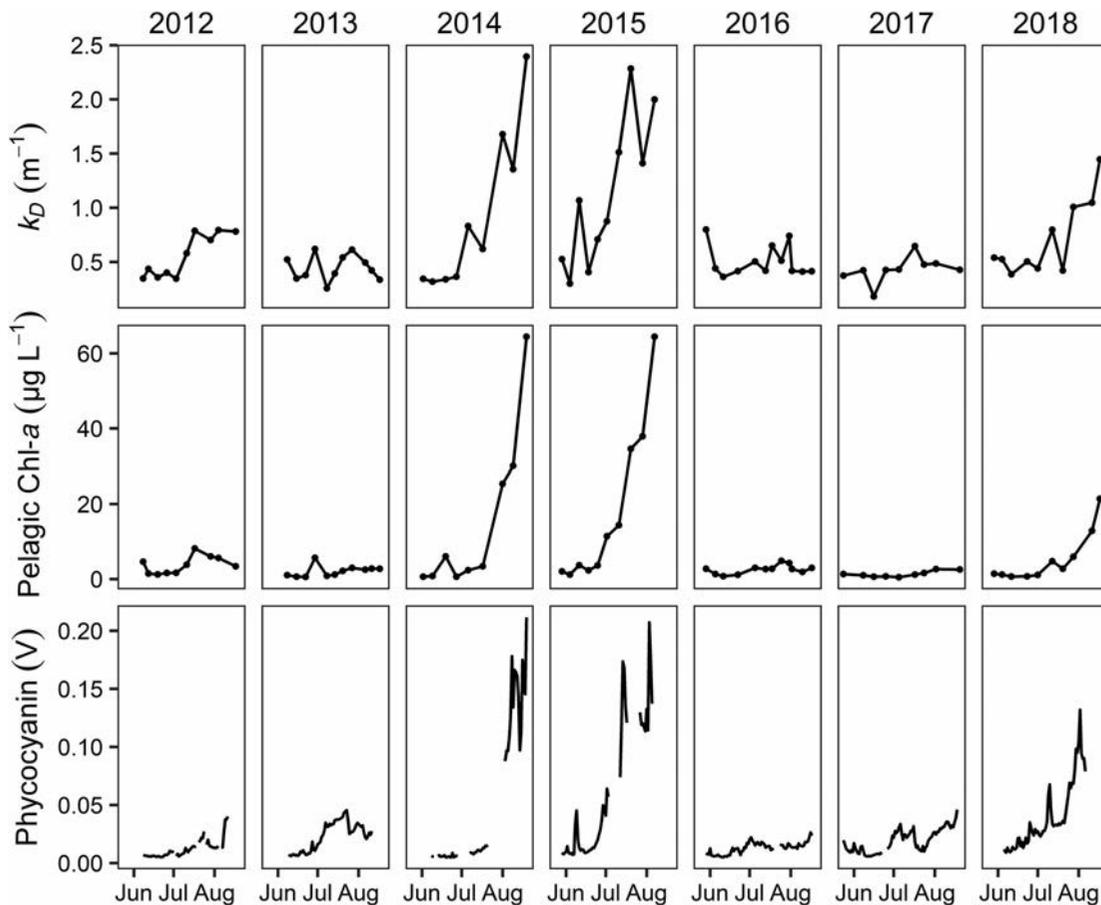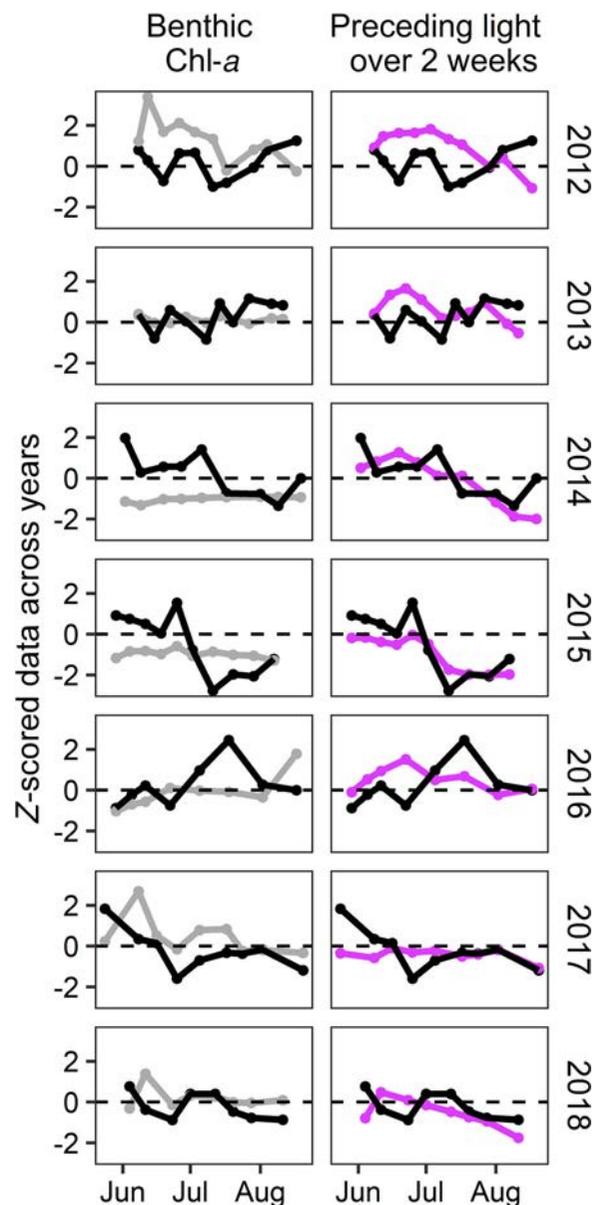

Figure 3. Temporal variation in water column clarity and phytoplankton abundance at our study site. Light attenuation coefficients (k_D) and pelagic Chl-*a* correspond to routine sample dates. Phycocyanin data are shown as daily averages (Volt: V) indicative of relative concentration. Gaps in the phycocyanin data are periods during which the sonde was inactive.
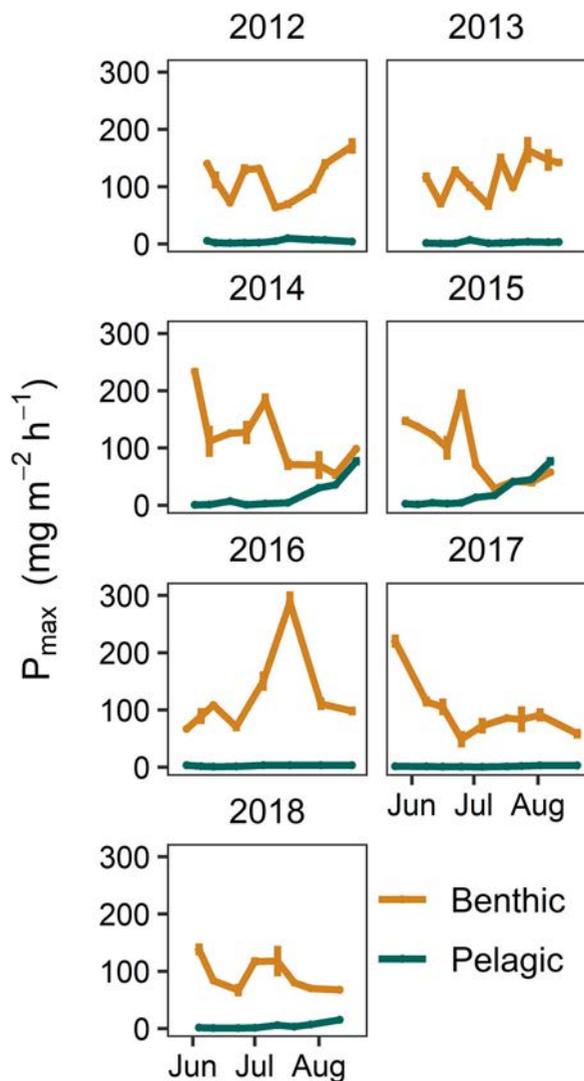
Figure 4. Temporal variation in benthic and pelagic maximum rates of primary production (P_{max}, measured as C). Standard errors are shown for each sample date and are based on standard errors from the dark and light replicate cores (benthic) or standard errors associated with the scaling factor, s, relating P_{max} to Chl-a (pelagic).


Figure 5. Interannual trends between standardized benthic P_{max} (black) and standardized explanatory variables: benthic Chl-a (gray) and the cumulative benthic light availability for the 2 weeks preceding the incubation (purple). For colour, see online version.

However, pelagic P_{max} approached or exceeded benthic P_{max} rates during the cyanobacteria blooms in 2014 and 2015 (Fig. 4).

Benthic P_{max} varied among and within summers, and we tested whether benthic Chl-a and recent light availability contributed to this variation. We found no significant influence of benthic Chl-a on benthic P_{max} (LRT: χ^2 < 0.01, df = 1, p = 0.999; Fig. 5), but the cumulative benthic light availability over the 2 weeks preceding the date of the sample significantly affected benthic P_{max} (LRT: χ^2 = 5.04, df = 1, p = 0.025). Low preceding benthic light availability was associated with low benthic P_{max} (Fig. 5). High preceding pelagic Chl-a concentrations and preceding phycocyanin values were also associated with decreases in benthic P_{max} (Supplemental Fig. S7).

The analyses that explain variation in benthic P_{max} using cumulative benthic light availability, pelagic Chl-a, and phycocyanin are not statistically independent because all 3 variables are related (Supplemental Material). Nonetheless, the analyses show that the same results are obtained using either mechanistic (light availability) or biotic (Chl-a or phycocyanin) variables.
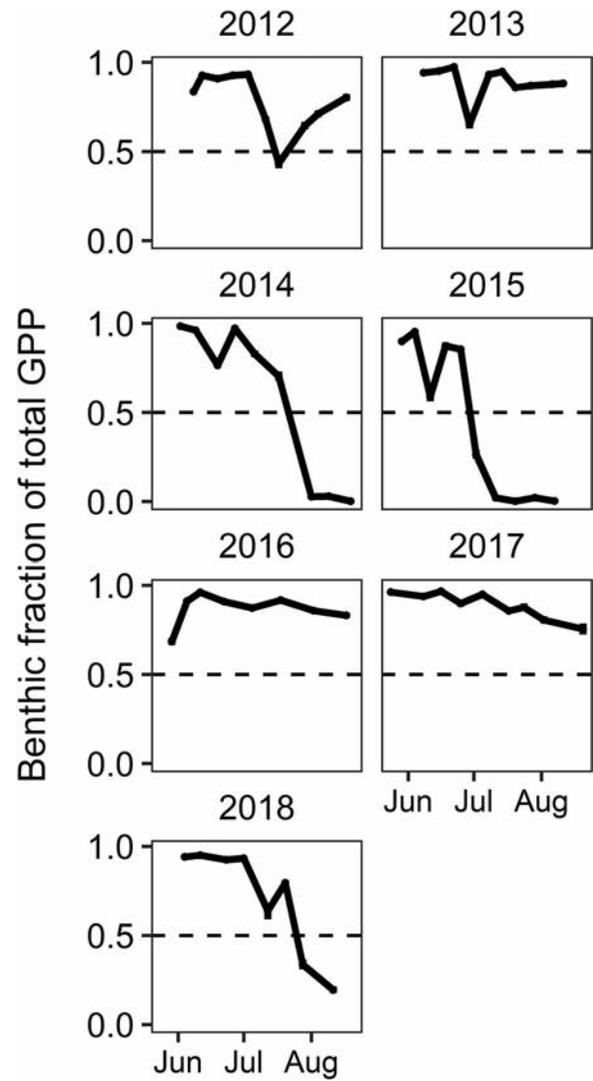
Partitioning of benthic and pelagic primary production

We estimated in situ benthic and pelagic GPP using the values of P_{max} from each sample date, the measured
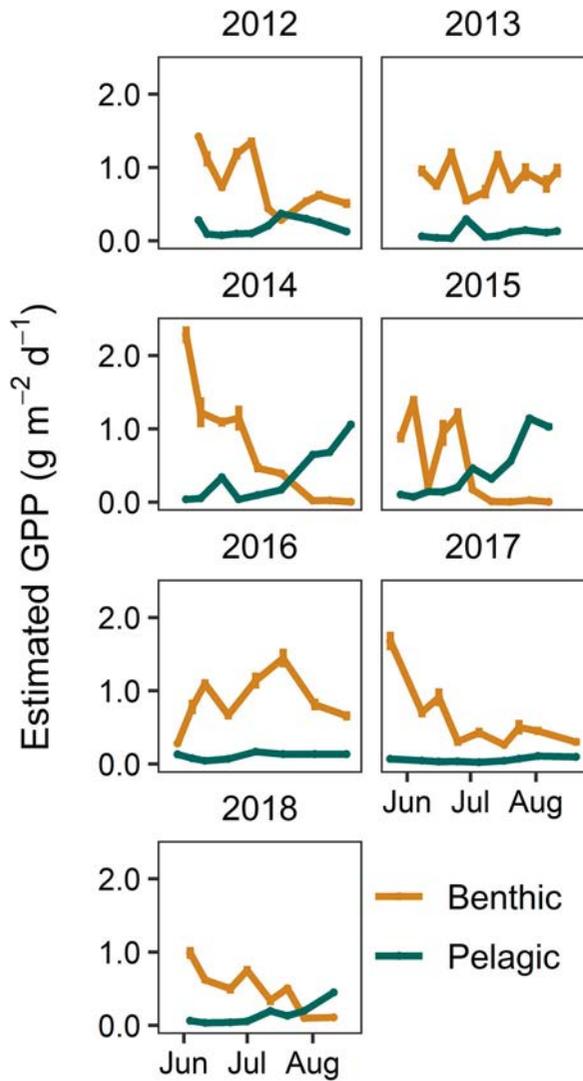
Figure 6. Temporal variation in estimated benthic and pelagic daily gross primary production (GPP, as C). Benthic and pelagic GPP was estimated using benthic and pelagic P_{max} rates, light attenuation coefficients, and incident light levels corresponding to a 1-week window around each sample date. Bars show propagated standard deviations. For colour, see online version.

Figure 7. The benthic fraction of total estimated production (daily benthic GPP divided by the sum of benthic and pelagic daily GPP) for the study site. Bars show propagated standard deviations.

light attenuation coefficients, and the corresponding mean incident light levels over a 1-week window. Estimated benthic GPP generally exceeded pelagic GPP, at times by an order of magnitude (Fig. 6). However, during periods of increased phytoplankton abundance, pelagic GPP exceeded benthic GPP and dominated primary production (Fig. 6, Supplemental Fig. S3). During times of elevated pelagic GPP, declines in benthic GPP can be attributed to immediate shading effects of phytoplankton (which increases water column light attenuation; Supplemental Fig. S5) as well as potential reductions to benthic P_{max}, which were associated with extended periods of low light availability. During clear-water conditions, variation in estimated benthic GPP can be partly attributed to variation in weekly

incident irradiance as well as variation in benthic P_{max} (Fig. 4 and 6).

The benthic fraction of total estimated production at our study site varied among and within summers. In all years, benthic primary production comprised most of the total production in early summer (late May through June), ranging from 59% to 99% (Fig. 7). In 2014, 2015, and 2018, there were marked declines in in the contribution of benthic producers toward total production, which reached <1% in 2014 and 2015 and <20% in 2018. In mid-2012, the contribution of benthic algae to total production fell slightly below 50% (Fig. 7) in conjunction with an uptick in estimated pelagic GPP, which may have been caused by high densities of *Oocystis* at this time (Bartrons et al. 2015). Otherwise, the contribution of benthic primary producers was never <64%

in the 4 years without dense cyanobacteria blooms (2012, 2013, 2016, 2017; Fig. 7).

We visualized how variation in benthic P_{max} and pelagic Chl-*a* influences total production and the partitioning of primary production (Fig. 8), showing 2 pathways through which increasing phytoplankton abundance may alter autotrophic structure. First, as phytoplankton biomass increases, in situ benthic GPP is expected to decrease due to lower water clarity

(Fig. 8a–b). However, the increase in pelagic GPP associated with increased phytoplankton biomass at least partially compensates for the declines in benthic GPP (Fig. 8c–d). Both the declines in benthic light availability and the increase in pelagic GPP reduce the relative contribution of benthic algae to total production (Fig. 8e–f).

Similar to previous modeling studies (Vadeboncoeur et al. 2008), this visualization suggests that benthic P_{max}
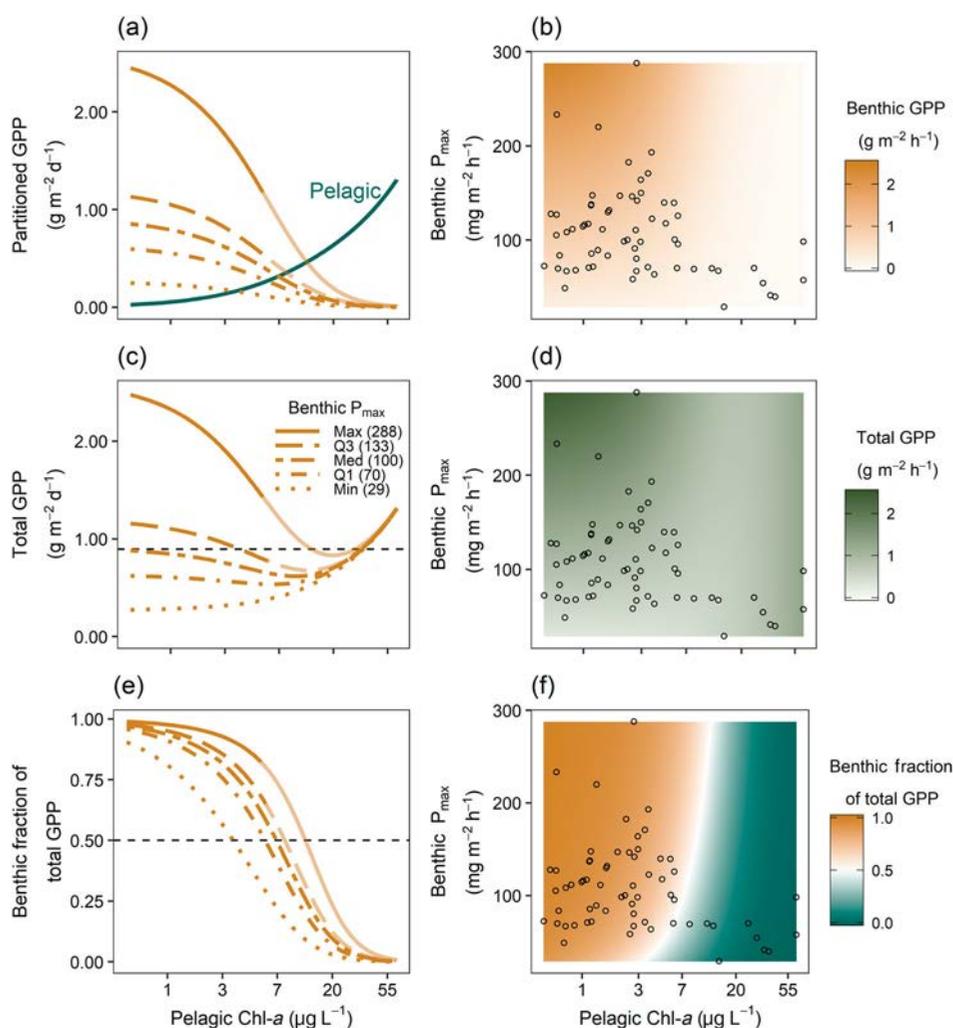
Figure 8. (a and b) Benthic gross primary production (GPP (measured as C)), (c and d) total GPP, and (e and f) the benthic fraction of total GPP were calculated for combinations of benthic P_{max} values and pelagic Chl-*a* concentrations as constrained by the variation in our data. Panels in the left column (a, c, e) focus on a subset of benthic P_{max} values (the minimum, first quartile, median, third quartile, and maximum C values: 29, 70, 100, 133, and 288 mg m^{-2} h^{-1}, respectively). Panels in the right column (b, d, f) include a continuous range of benthic P_{max} values. Pelagic Chl-*a* concentrations were translated into light attenuation coefficients using an empirical model fit to our data from 2012 to 2018. We used average diel incident light levels to standardize external light conditions for this visualization. Points (panels b, d, f) depict the observed combinations of benthic P_{max} values and pelagic Chl-*a* concentrations. In panel (a), a single line depicts pelagic GPP because it is unaffected by benthic P_{max}. The horizontal line in panel (c) represents the mean daily total GPP estimated across all our sampling dates. The horizontal line at 50% in panel (e) represents the point at which benthic and pelagic algae equally contribute to total GPP. A lighter shade line (panels a, c, e) approximately delineates where the visualization extrapolates pelagic Chl-*a* beyond typically observed concentrations. For the maximum benthic P_{max} value, this occurs at 5.57 µg L^{-1}, the maximum pelagic Chl-*a* concentration corresponding to the top quartile of benthic P_{max} values (b, d, f), and for the third quantile benthic P_{max} value, this occurs at 6.01 µg L^{-1}, the maximum pelagic Chl-*a* concentration corresponding to the top 2 quartiles of benthic P_{max} values (b, d, f). Pelagic Chl-*a* concentrations are shown on a natural-log scale. For colour, see online version.

affects the point at which autotrophic structure shifts from benthic dominated to pelagic dominated. At low to intermediate pelagic Chl-*a* concentrations, declines in benthic GPP are less substantial when benthic P_{max} is high (Fig. 8a–b). Therefore, pelagic GPP surpasses benthic GPP at a lower phytoplankton biomass when benthic P_{max} is low compared to when it is high (Fig. 8a). For low benthic P_{max} values, increased phytoplankton biomass resulted in maintenance or increase of total GPP; however, for high benthic P_{max} values, total GPP declined at low to intermediate phytoplankton biomass (Fig. 8c–d), indicating that the increased pelagic GPP was not fully compensating for declines in benthic GPP. Assuming our highest observed benthic P_{max} values, phytoplankton biomass would not fully compensate for declines in benthic GPP over our observed range of pelagic Chl-*a* concentrations (Fig. 8c–d). However, note that we did not observe high benthic P_{max} rates when pelagic Chl-*a* concentrations were high in our actual data (demonstrated by the light line coloration in Fig. 8a, c, and e and raw data points in Fig. 8b, d, and f), consistent with the influence of previous benthic light availability on benthic P_{max}. Similarly, for low benthic P_{max} values, the benthic fraction of total production is expected to decline below 50% at a lower phytoplankton abundance (and correspondingly higher water clarity) than if P_{max} is high (Fig. 8e–f).

Discussion

Autotrophic structure is a foundational characteristic of lakes, with shifts in the partitioning of primary production into benthic and pelagic components potentially influencing multiple dimensions of ecosystem function. We examined benthic and pelagic primary production of a shallow, subarctic lake in which autotrophic structure exhibited substantial temporal variability within and among summers. For our study site, the capacity for benthic primary producers to contribute to total primary production typically exceeds that of phytoplankton on an areal basis, based on the differences in benthic and pelagic P_{max} rates. Consequently, benthic algae dominated total GPP during relatively clear-water periods, but during cyanobacterial blooms, pelagic GPP dominated total production. Similarly, a recent study that examined ecosystem metabolism (integrated across pelagic and benthic habitats) from 2012 to 2018 at the same study site showed that cyanobacteria blooms contributed to the temporal variation in whole-ecosystem production (Phillips 2020). When dense cyanobacteria blooms spread through much of Mývatn in 2014, 2015, and 2018, the benthic fraction of total production rapidly declined. The declines in

estimated benthic GPP and its contribution to total production were strongly linked to reductions in light availability associated with increased phytoplankton abundance. Thus, while Mývatn's autotrophic structure is often benthic dominated, strong competitive effects of phytoplankton on benthic primary producers can shift the partitioning of total production.

Benthic P_{max} values spanned an order of magnitude, representing large variation in the maximum photosynthetic potential of benthic primary producers. We investigated the recently experienced light environment as a possible explanation for the large variation in benthic P_{max}. Benthic light availability over a 2-week period had a moderate effect on benthic P_{max}. Low levels of recent light availability were associated with lower benthic P_{max}, despite the possibility of increased photosynthetic efficiency (e.g., due to increased intracellular Chl-*a* content) that can occur in light-limited conditions (Falkowski and LaRoche 1991). Complementary analyses examining preceding pelagic Chl-*a* concentrations or phycocyanin values showed a similar effect on benthic P_{max} but in terms of biotic pelagic drivers: algal and cyanobacterial abundance. These results suggest that phytoplankton can adversely affect benthic production not only by immediately decreasing light availability, but also by potentially reducing the photosynthetic potential of benthic primary producers due to prolonged shading. However, negative effects of light limitation on benthic P_{max} may be disrupted in Mývatn because cyanobacteria blooms tend to be ephemeral, and the lake does not maintain a pelagic-dominated autotrophic structure long term (i.e., across years).

We also examined whether benthic Chl-*a* concentrations were associated with benthic P_{max} and found no relationship between them. The absence of an association between benthic Chl-*a* and P_{max} might indicate that Chl-*a* concentration is not a reliable surrogate for benthic algal biomass, as suggested by discrepancies between benthic Chl-*a* and algal biovolume (Baulch et al. 2009). Furthermore, our sampling of the top 0.75 or 2 cm (2014, 2015, and early 2016) layer of sediment likely included non-photosynthetically active chlorophyll (Cyr 1998, Liboriussen and Jeppesen 2003), which may further complicate using benthic Chl-*a* as a surrogate for the biomass of photosynthetically active algae for epipelic communities. Thus, the absence of an association between benthic Chl-*a* and benthic P_{max} does not necessarily imply that P_{max} is unaffected by photosynthetically active algal biomass.

Previous modeling studies have highlighted the influence of maximum benthic productivity rates on autotrophic structure (Vadeboncoeur et al. 2008, Genkai-Kato

et al. 2012, Brothers et al. 2016). Because benthic P_{max} measurements are relatively rare, models have relied on published P_{max} values that may span multiple lakes, substrates, and environmental conditions. By exploring the relationship between benthic P_{max} and autotrophic structure across an empirically observed parameter space, our findings complement those of previous theoretical models by demonstrating that variation in benthic P_{max} within a single lake can affect the point (i.e., the biomass of phytoplankton and associated reductions to benthic light availability) at which autotrophic structure shifts from benthic dominated to pelagic dominated. This shift may have consequences for ecosystem processes such as energy flow because the contributions of benthic and pelagic primary production can alter consumer reliance on benthic or pelagic-derived carbon (Turschak et al. 2014, Stewart et al. 2017).

Changes in autotrophic structure may result in compensatory shifts in production such that decreased primary production in one habitat would be compensated for by increased production in the other, thereby maintaining constant rates of whole-system productivity (Vadeboncoeur et al. 2001, Brothers et al. 2016, Genzoli and Hall 2016). Conversely, shifts in autotrophic structure may cause declines in total production if the increased primary production in one habitat does not equal the declines in primary production in the other (Karlsson et al. 2009, Higgins et al. 2014). Similar to previous studies (Genkai-Kato et al. 2012, Brothers et al. 2016), our visualization across hypothetical combinations of benthic P_{max} and pelagic algal biomass illustrates the role of benthic P_{max} in shaping the overall effect that a shift in autotrophic structure has on total GPP. We found that phytoplankton are more likely to compensate for shading-induced declines in benthic GPP if benthic P_{max} is low. By contrast, even the highest pelagic Chl-a concentrations we observed are unlikely to offset declines in benthic GPP associated with high benthic P_{max}. This conclusion, however, must be made with caution because our maximum observed benthic P_{max} (C: 288 mg m^{-2} h^{-1}) was not frequently observed; nonetheless, similarly high values have been reported in other shallow lakes (Liboriussen and Jeppesen 2003). Also, we did not observe high benthic P_{max} values when pelagic Chl-a concentrations were high, such as during dense cyanobacteria blooms (i.e., raw data points in Fig. 8). Thus, it is unclear whether paired occurrences of high phytoplankton biomass and high benthic photosynthetic capacity are likely in Mývatn.

Cyanobacteria blooms were a central determinant of temporal variation in autotrophic structure, but the factors influencing variation in their intensity are not fully understood. High wind events in early summer can trigger phosphate release from Mývatn's sediment, thereby promoting advantageous conditions for N-fixing cyanobacteria (Einarsson et al. 2004). However, associations between windstorms and dense cyanobacteria blooms are not necessarily consistent. For example, in 2 consecutive years with early summer sediment resuspension events and associated phosphate release, a cyanobacteria bloom only developed in one of the years (Einarsson et al. 2004). Likewise, high wind events in early summer were not always associated with dense cyanobacteria blooms in our study (Supplemental Fig. S1). Mývatn supports high densities of chironomid larvae, which may mitigate the release of phosphate to the water column by stabilizing and oxygenating the sediment through their tube-building and bioturbation behaviors (Ólafsson and Paterson 2004, Holker et al. 2015). Thus, chironomid population crashes and intense cyanobacteria blooms are potentially associated (Einarsson et al. 2004). However, our study does not include any years with low lake-wide abundances of chironomid larvae, making it difficult to assess this potential association. While the mechanisms influencing cyanobacteria blooms in Mývatn may involve both internal dynamics and external drivers, they require further investigation.

Theoretical work on benthic–pelagic coupling predicts that shallow lakes with large phosphorus pools in the sediment should be able to shift between regimes dominated by phytoplankton and periphyton (Genkai-Kato et al. 2012). Movement from one state to the other is facilitated by positive feedback loops in which amassing phytoplankton biomass continually shades benthic algae, thereby enhancing nutrient release from the sediment and further increasing pelagic production (Liboriussen and Jeppesen 2003, Genkai-Kato et al. 2012, Jäger and Diehl 2014). Mývatn has relatively high P loading rates (4.1 mg m^{-2} d^{-1}) from groundwater inputs (Ólafsson 1979a). Additionally, cyanobacteria bloom duration can reach 88 days (Jónasson and Adalsteinsson 1979) and exceed the lake's 27-day residence time, suggesting that prolonged growth can be sustained in the lake. Nonetheless, no records exist of multi-year regime shifts to a turbid state caused by cyanobacteria dominance in Mývatn. Several characteristics of Mývatn may reduce the likelihood of regime shifts. First, the sediment interface at Mývatn may remain oxic regardless of benthic photosynthesis because the lake is shallow and well mixed. Therefore, even when there is shading from phytoplankton and hence little oxygen production from benthic photosynthesis, release of phosphate from the sediment may be minimal, potentially culminating in phosphate limitation. If *Dolichospermum* growth rates eventually slow

as the bloom progresses (e.g., due to nutrient limitation), the lake's high flushing rates associated with the short residence time may remove colonies more quickly than they grow and contribute to cyanobacteria bloom termination. Similarly, previous studies have proposed short residence times as a factor limiting the dominance of phytoplankton in estuaries and coastal areas (Valiela et al. 1997, Cebrian et al. 2014). In summary, the positive feedback cycle underlying regime shifts between periphyton- and phytoplankton-dominated states may be decoupled in Mývatn, thereby preventing a shift to a multi-year turbid state.

Our study did not assess seasonal variation in primary production. Logistical constraints and long ice-cover duration (Oct–May) largely constricted our data collection to summer. However, our focus on summer likely captured periods with the strongest variation in autotrophic structure because phytoplankton production peaks during this season (Jónasson and Adalsteinsson 1979). Additionally, secondary production is high in the summer growing season, such that summer shifts in autotrophic structure are most likely to impact energy flow. Nonetheless, seasonally extensive data may reveal further insights into patterns of primary production. For example, light transmissivity through ice may influence the photosynthetic potential of benthic algae shortly after ice off. Seasonal data may also reveal how summer primary production influences other ecosystem processes. For example, cyanobacteria may influence nutrient cycling by releasing inorganic nitrogen, with the potential to support autumn blooms of other phytoplankton taxa (e.g., diatoms and chrysophyceans; Ólafsson 1979a).

This study highlights the changes in the partitioning of primary production between benthic and pelagic habitats in a shallow lake. Despite the potential for phytoplankton to compensate for declines in benthic GPP, a shift in autotrophic structure may nonetheless be consequential in systems (including Mývatn) where consumers heavily rely on benthic energy pathways (Hampton et al. 2011, Vander Zanden et al. 2011). While monitoring temporal variation in lake autotrophic structure under ambient conditions is not commonly undertaken (but see Liboriussen and Jeppesen 2003, Althouse et al. 2014), Mývatn shows that autotrophic structure is dynamic during summer both within and across years. Therefore, it would be misleading to characterize its autotrophic structure without accounting for temporal variation. Many other lakes, especially those that are shallow, may also share inherent temporal variation in autotrophic structure, and understanding these dynamics may assist in predicting the response of aquatic ecosystems to ongoing and future environmental changes.

ORCID

Amanda R. McCormick http://orcid.org/0000-0002-1742-0867
Joseph S. Phillips http://orcid.org/0000-0003-2016-1306
Jamieson C. Botsch http://orcid.org/0000-0003-0670-9785
Anthony R. Ives http://orcid.org/0000-0001-9375-9523

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