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## LETTER

# Phenological mismatch in coastal western Alaska may increase summer season greenhouse gas uptake

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Supplementary material for this article is available [online](#)

## Abstract

High latitude ecosystems are prone to phenological mismatches due to climate change- driven advances in the growing season and changing arrival times of migratory herbivores. These changes have the potential to alter biogeochemical cycling and contribute to feedbacks on climate change by altering greenhouse gas (GHG) emissions of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) through large regions of the Arctic. Yet the effects of phenological mismatches on gas fluxes are currently unexplored. We used a three-year field experiment that altered the start of the growing season and timing of grazing to investigate how phenological mismatch affects GHG exchange. We found early grazing increased mean GHG emission to the atmosphere despite lower CH<sub>4</sub> emissions due to grazing-induced changes in vegetation structure that increased uptake of CO<sub>2</sub>. In contrast, late grazing reduced GHG emissions because greater plant productivity led to an increase in CO<sub>2</sub> uptake that overcame the increase in CH<sub>4</sub> emission. Timing of grazing was an important control on both CO<sub>2</sub> and CH<sub>4</sub> emissions, and net GHG exchange was the result of opposing fluxes of CO<sub>2</sub> and CH<sub>4</sub>. N<sub>2</sub>O played a negligible role in GHG flux. Advancing the growing season had a smaller effect on GHG emissions than changes to timing of grazing in this study. Our results suggest that a phenological mismatch that delays timing of grazing relative to the growing season, a change which is already developing along in western coastal Alaska, will reduce GHG emissions to the atmosphere through increased CO<sub>2</sub> uptake despite greater CH<sub>4</sub> emissions.

## Introduction

The potential for phenological mismatches between consumers and their resources as a result of changing climate is particularly acute in high latitude regions where the growing season is advancing rapidly due to increasing temperatures (Serreze and Francis 2006, Barber *et al* 2008, IPCC 2013). In these regions, herbivores that time their migration using photoperiod or cues in their wintering habitat that are not directly related to temperature in their summer habitat, may arrive late relative to vegetation phenology thus altering the timing of their

grazing with respect to the growing season (Doiron *et al* 2015, Clausen and Clausen 2013). Both herbivory and the timing of the growing season are important controls on biogeochemical cycling and greenhouse gas (GHG) emissions from high latitude regions (Humphreys and Lafleur 2011, Cahoon *et al* 2016, Metcalfe and Olofsson 2015, Kelsey *et al* 2016). Therefore the interacting effects of changes to the start of the growing season and grazing phenology may have implications for regional GHG budgets. However, the effect of a phenological mismatch on GHG exchange in high latitude ecosystems remains unexamined.

Phenological mismatch between grazing and the growing season has the potential to alter regional GHG fluxes by changing the local environmental conditions that control gas exchange. An earlier or prolonged growing season at high latitudes may increase CO<sub>2</sub> uptake by promoting vegetation growth and increasing primary productivity (Cahoon *et al* 2016, Ueyama *et al* 2013). However, the effects of grazing may counteract an advanced growing season because grazing decreases biomass (Sjögersten *et al* 2008) and reduces net CO<sub>2</sub> uptake (Sjögersten *et al* 2012, Cahoon *et al* 2012), despite the potential for increased CO<sub>2</sub> emission through soil respiration in response to less shading and warmer soil temperatures (Risch *et al* 2013, Welker *et al* 2004). In contrast, some grazing exclusion studies in high latitude systems suggest the opposite response with grazing exclusion resulting in greater CO<sub>2</sub> emission, particularly where there is a change in species composition in response to the removal of grazing (Falk *et al* 2015, Metcalfe and Olofsson 2015, Lara *et al* 2017). While the mechanisms are complex, it is clear that presence or absence of grazing is an important driver of CO<sub>2</sub> flux through effects on soil and vegetation properties, and changes in timing of grazing is also likely an important control on local CO<sub>2</sub> flux.

Phenological mismatch may also alter CH<sub>4</sub> and N<sub>2</sub>O fluxes from northern ecosystems. Anoxic soils within northern wetlands are a source of CH<sub>4</sub> that may increase with warming and contribute to a GHG source (Bousquet *et al* 2011, Turetsky *et al* 2014, Bloom *et al* 2010), particularly in regions influenced by herbivory (Kelsey *et al* 2016). Grazing can also increase CH<sub>4</sub> flux by decreasing diffusive resistance to CH<sub>4</sub> transport through plant biomass (Dingemans *et al* 2011). Conversely, grazing can reduce CH<sub>4</sub> fluxes by decreasing biomass and slowing the delivery of carbon to the soil (Ding *et al* 2005, Chen *et al* 2014), or through changes to species composition (Falk *et al* 2015). Northern wetlands also produce N<sub>2</sub>O under the appropriate soil moisture, temperature and nutrient conditions (Ma *et al* 2008, Tian *et al* 2012, Stewart *et al* 2014). Few studies have investigated effects of herbivory on N<sub>2</sub>O, but research indicates trampling and fecal input can increase the rates of N cycling (Zacheis *et al* 2002, Oenema *et al* 1997, Gao *et al* 2008), which could influence N<sub>2</sub>O flux. These results suggest grazing and growing season conditions can affect GHG fluxes, but how timing of grazing and growing season onset will influence these processes remains an important outstanding question.

The coastal region of the Yukon-Kuskokwim (Y-K) Delta in western Alaska is experiencing rapid climate change that has created a phenological mismatch between the start of the growing season and grazing by the primary herbivores of the region, migratory geese. Over the last 30 years increasing temperatures have led to an advance in the onset of the growing season of 2.6 days per decade (determined from

50% of maximum normalized difference vegetation index, D. Douglas, unpubl. data, methods described in Ross *et al* 2017). In contrast, the hatch date of Pacific black brant (*Branta bernicla nigricans*), which marks the start of the intense grazing season of the most prominent grazers at this site, has advanced only 1.4 days per decade (Fischer *et al* 2017). These changes have resulted in a phenological mismatch of 4 days since the early 1980s such that the geese start to graze 'late' relative to the growing season. The goal of this research is to determine how such a trophic mismatch affects GHG fluxes. We used a field experiment with controlled conditions to manipulate the start of the growing season and the timing of grazing to investigate the following questions: (1) How does change in the timing of grazing relative to the growing season alter GHG fluxes? (2) What are the controls on each component of GHG exchange (i.e. CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O) in this system? The results of this study will help determine how changing phenology of vegetation and grazing interact as controls on GHG emissions, and the potential implications for phenological mismatch to alter GHG exchange in high latitude ecosystems.

## Materials and methods

### Study site

This study was conducted in the central coastal region of Y-K Delta in western Alaska (61.247°N, -165.616°W; supplemental figure 1 available at [stacks.iop.org/ERL/13/044032/mmedia](https://stacks.iop.org/ERL/13/044032/mmedia)). The Y-K Delta is composed of 75 000 km<sup>2</sup> of coastal tundra along the Bering Sea, between the Yukon and Kuskokwim Rivers. Vegetation in the coastal region is characterized by a gradient from the barren tidal mud flats, to wet sedge meadows dominated by *Carex*, to moist meadows on slough levees (Jorgenson 2000). Permafrost is absent in the coastal region of the Y-K Delta where this study site is located. Our study site is located within a colony of Pacific black brant (brant hereafter) that use the area as nesting and brood rearing habitat. Brant, and the other primary grazers at this site, cackling geese (*Branta hutchinsii*), do not grub during the breeding season rather they eat only aboveground parts of the local *Carex* vegetation (Sedinger and Raveling 1984), and their grazing results in the formation of grazing lawns.

### Experimental design

Our study was a field experiment with a factorial design consisting of four timing of grazing treatments (early, typical, late and no grazing) crossed with two timing of growing season treatments (advanced and ambient) for a total of eight treatments. Our experiment also included 'background' grazing plots (table 1) that were naturally grazed through the summer and fall. Timing of grazing was manipulated using captive brant and was designed to align with the timing of

**Table 1.** Description of study design indicating how timing of grazing and growing season treatments contribute to phenological mismatch. Typical grazing is matched with long-term historical means, early and late grazing started respectively 21 days before and after typical grazing. Advanced spring was estimated to be 22 days early (supplemental figure 2). The typical grazing, advanced growing season scenario is the most likely consequence of climate change.

Grazing	Growing season	Result	Mismatch?
Early	Ambient	Geese arrive 21 days early; spring typical	Early grazing
Early	Advanced	Geese arrive 21 days early; spring 22 days early	No mismatch
Typical	Ambient	Geese arrive typical time; spring typical	No mismatch
Typical	Advanced	Geese arrive typical time; spring 22 days early	Late grazing
Late	Ambient	Geese arrive 21 days late; spring typical	Late grazing
Late	Advanced	Geese arrive 21 days late; spring 22 days early	Late grazing
None	Ambient	Geese do not arrive; spring 22 days early	No grazing
None	Advanced	Geese do not arrive; spring typical	No grazing
Control	Ambient	No treatment	Ambient conditions

maximal use of the grazing lawns. The start of the early and late treatments differed by 21 days from the start of typical grazing on 20 June (Fischer *et al* 2017) to simulate several scenarios of phenological mismatch: both where grazing is early relative to the growing season (early grazing, typical growing season), and the more likely scenario for this region where grazing occurs late relative to the growing season (typical grazing, advanced growing season). All treatments were grazed at the same intensity: two geese for four 24 hour periods, two weeks apart, which is equal to 7.2 goose-hours  $m^{-2}$  month $^{-1}$  (comparable to Herzog and Sedinger 2004). The background grazing plots were naturally grazed throughout the summer. Prior to each round of grazing geese were held without food for two hours to allow any feces from captive feed to pass through their digestive system (Prop and Vulink 1992). The birds were also held for an additional two hours after grazing in order to recover and return any feces deposited to the appropriate experimental plots.

The start of the growing season was manipulated using passive open-topped chambers (OTCs; 85 cm base diameter base tapering to 50 cm diameter top, 30 cm tall) that warmed the soil from 1 May until 1 July each season. While often used to increase temperature, OTCs also accelerate growth at the start of the season (Sullivan and Welker 2005, Post *et al* 2008). Therefore, OTCs were left on plots long enough to advance the growing season but not have season-long warming effects. OTCs were temporarily removed for 24 hours at a time during goose grazing treatments before their permanent removal on July 1. The OTCs advanced the growing season by 22 days (supplemental figure 2).

Our study was composed of six experimental blocks established within grazing lawns. Each block contained a replicate plot of all eight treatments plus the background for a total of 54 plots, each ca. 1.13  $m^2$  (supplemental figures 3(a) and (b)). The treatments were initiated in May 2014 and remained in place for three summers; measurements for this study were done during the third year of treatment. To remove background grazing, exclosures were installed around all treatment plots from 1 May through 25 August. Exclosures were designed to surround two plots at a time according to the implementation of the grazing treatment (i.e. the advanced growing season, early grazing plot was grazed

at the same time as the ambient growing season, early grazing plot; supplemental figures 3(c) and (d)).

### Greenhouse gas measurements and environmental conditions

GHG exchange was measured approximately two times per week at each plot between 2 June and 18 August 2016 for a total of 18 dates for  $CO_2$  and 19 dates for  $CH_4$  and  $N_2O$ . Flux chamber collars were installed in each plot in early May. The collars (10 cm tall, 15 cm diameter) were inserted approximately 5 cm into the soil, left in place for more than 48 hours before measurement and remained in the ground undisturbed all season. A chamber (21 cm tall, 13 cm diameter, with a 5 cm flange around the base) was used to measure gas exchange. During measurement the chamber was attached to the collar to create a gas-tight seal, and a fan was used inside the chamber to avoid stratification. All gas exchange measurements were made within 5 hours of solar noon.  $CO_2$  exchange was measured on five blocks (45 plots), and  $CH_4$  and  $N_2O$  exchanged were measured concurrently on three blocks (27 plots). Due to constraints on how the equipment could be moved around the field site, one block that was measured for  $CH_4$  and  $N_2O$  exchange was not measured for  $CO_2$  fluxes.  $CO_2$  exchange was occasionally measured on different dates than  $CH_4$  and  $N_2O$  exchange, and therefore the measurement dates were organized into sampling occasions for the purpose of statistical analyses.

Measurements of  $CO_2$  exchange were made by circulating gas from the chamber to an infrared gas analyzer (supplemental table 1). Net ecosystem exchange (NEE) was measured using a translucent chamber. After the translucent chamber was removed from the collar and allowed to equilibrate with the ambient atmosphere, the chamber was placed back on the collar and covered with an opaque cloth to obtain a measurement of ecosystem respiration (ER).  $CO_2$  flux was calculated using an exponential model of change in concentration through time between 30s to 120s after deployment. The difference between ER and NEE was used to determine gross primary productivity (GPP).  $CH_4$  and  $N_2O$  exchange were measured by circulating gas from the chamber to a cavity ring-down spectroscopy analyzer.  $CH_4$  and  $N_2O$  concentrations were

measured every 5 seconds for 3 minutes. CH<sub>4</sub> and N<sub>2</sub>O fluxes were determined using the change in concentration through time between approximately 60s and 180s after chamber deployment using a non-linear model specifically designed for these gases (Hutchinson and Mosier 1981). All fluxes were corrected for water content. Mean combined GHG emissions expressed in CO<sub>2</sub> equivalents were determined using the 100 year horizon global warming potential of 34 for CH<sub>4</sub>, and 298 for N<sub>2</sub>O (Myhre *et al* 2013). Seasonal mean GHG flux in CO<sub>2</sub> equivalents was calculated by multiplying the seasonal mean flux by the global warming potential for each gas.

Local environmental and soil conditions were measured through a combination of *in situ* measurements and continuous sensors with data loggers (supplemental table 1). A local meteorological station collected continuous measurements of air temperature at 2 m, precipitation at 0.5 m, and photosynthetically available radiation (PAR) at 2.5 m. Soil temperature at each plot was measured 10 cm below the soil surface. *In situ* measurements of vegetation height within the collars were made every 10 days throughout the season. Total biomass within each flux collar was determined at the end of the study by harvesting and obtaining a dry weight.

### Statistical analyses

To assess the effectiveness of our advanced growing season treatments, we determined that our treatment advanced the season by ca. 22 days (already presented in supplemental figure 2). To assess the effectiveness of our grazing treatments we compared GHG fluxes among the timing of grazing treatments and the background plot using analysis of variance (ANOVA).

To explore how phenological mismatch affects GHG fluxes (Question 1), and controls on CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O exchange (Question 2), we used a linear mixed modeling framework with GHG flux as the response variable, soil temperature, air temperature, PAR, biomass, and stem height as continuous predictor variables, timing of growing season and timing of grazing treatments as categorical predictor variables, and block and sampling occasion as random effects. The most important variables were determined as those present in the best performing model. For each GHG we tested 41 different models plus a null model (lmer function in the R package lme4 (Bates *et al* 2015 R Core Development Team), supplemental table (2)). All models included only biologically relevant predictor variables. Models were restricted *a priori* to two terms or fewer, or three terms when an interaction was present, according to the number of observations in our dataset (Bolker *et al* 2009). Each model suite included all possible combinations of predictor variables, both with and without interactions. Covarying predictors, including air temperature and soil temperature, and biomass and stem height, were not included in the same model. The typical-ambient plots were

coded as the reference level for categorical variables. CH<sub>4</sub> and N<sub>2</sub>O fluxes were log-transformed to produce a normal distribution prior to analysis. Continuous predictor variables were centered and scaled to produce a standard deviation of one and a mean of zero. The predictor variables met assumptions of non-collinearity and the residuals met assumptions for normality and homogeneity of variance. Model performance was evaluated by the Akaike Information Criteria (AIC; MuMIn package, Bartón K 2014, R Core Development Team). We based our model selection on AIC because it is preferred for selecting among multiple incompletely specified models (Aho *et al* 2014). We determined goodness-of-fit using a pseudo  $r^2$  calculated according to the recommendation of Nakagawa and Schielzeth (2013).

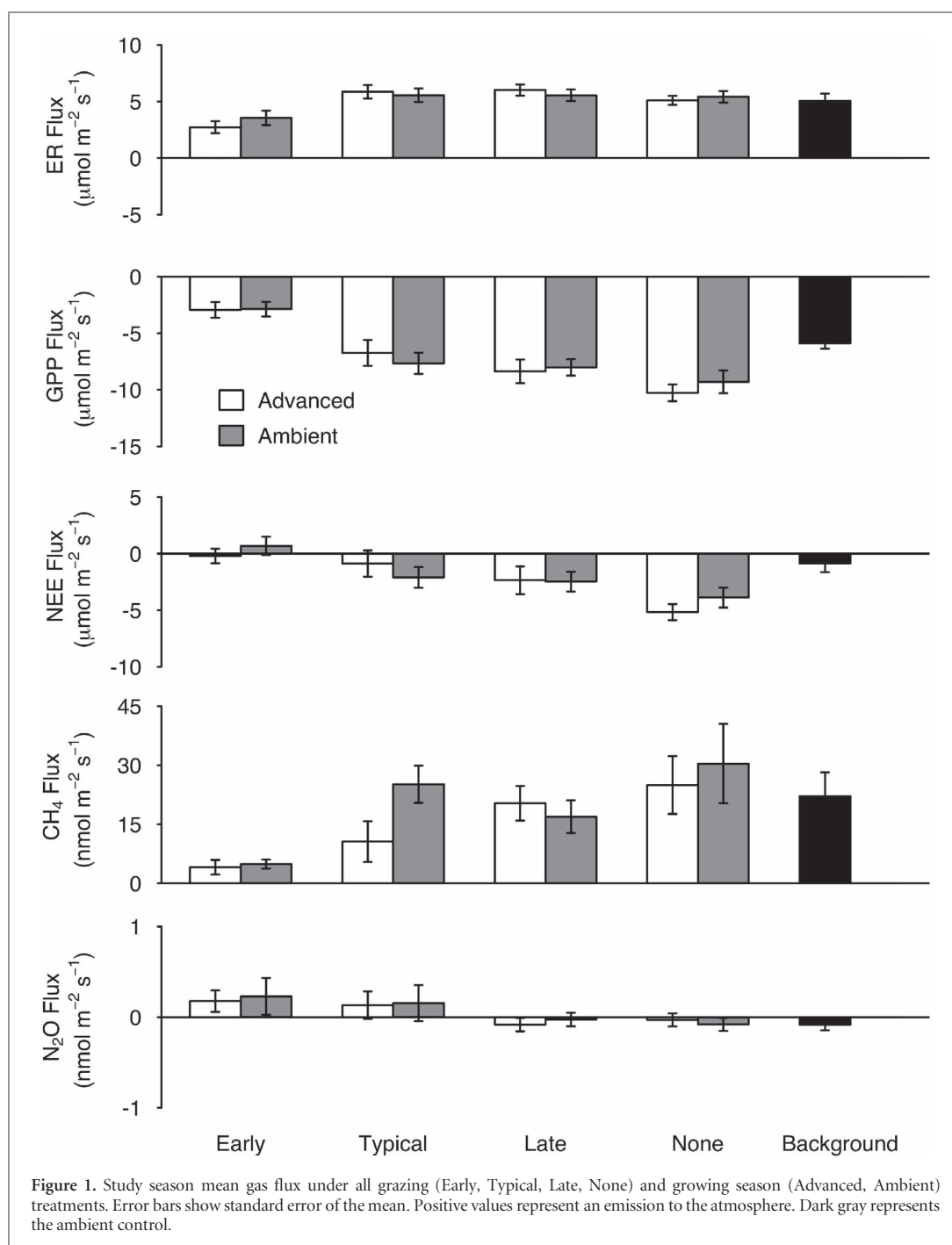
## Results

### CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O exchange

Our results confirm this study design as a robust method for testing the effects of changing phenology on GHG fluxes because we did not identify any differences in CO<sub>2</sub>, CH<sub>4</sub> or N<sub>2</sub>O gas exchange between typical grazing treatments and the background plots (supplemental table 3). Despite seasonal trends in temperature and solar radiation (supplemental figure 4), our measurements of GHG exchange all showed little trend through the season in CO<sub>2</sub>, CH<sub>4</sub> or N<sub>2</sub>O fluxes (supplemental figure 5). We found that advancing the growing season resulted in a small reduction in CO<sub>2</sub> uptake (less negative NEE; figure 1) but timing of grazing had a larger and more consistent effect on CO<sub>2</sub> exchange (table 2, supplemental table 4). Early grazing was the only grazing treatment that reduced CO<sub>2</sub> uptake (less negative NEE) because it increased ER more than it decreased GPP. In contrast, late grazing increased CO<sub>2</sub> uptake (more negative NEE) as a result of greater GPP accompanied by only slight increases in ER (figure 1). CO<sub>2</sub> uptake increased the most in response to no grazing because of large increases in GPP.

Our modeling results suggest that GPP overwhelmed ER to control NEE. Both GPP and NEE were driven by nearly the same environmental factors: PAR, vegetation size (biomass and stem height respectively), and their interaction indicating that CO<sub>2</sub> exchange was more strongly related to PAR in tall vegetation (pseudo  $r^2 = 0.60$  and  $0.51$  respectively; table 2). In contrast, ER was driven by soil temperature and timing of grazing (pseudo  $r^2 = 0.68$ ).

Timing of the growing season had no consistent influence on mean CH<sub>4</sub> emissions, but timing of grazing did influence CH<sub>4</sub> flux (figure 1). Early grazing had the lowest CH<sub>4</sub> emissions, and emissions increased through typical, late and no grazing (figure 1). The importance of grazing timing in controlling CH<sub>4</sub> emissions was confirmed further by our modeling.



The best performing model of CH<sub>4</sub> flux (pseudo  $r^2 = 0.74$ ) included biomass and timing of grazing (table 2).

The best performing model of N<sub>2</sub>O flux contained soil temperature, biomass, and their interaction, but was quite weak (table 2; pseudo  $R^2 = 0.08$ ). The interaction of soil temperature and plant biomass suggests that plots with less vegetation have higher N<sub>2</sub>O emissions, particularly when soil temperatures are warm.

### Seasonal global warming potential

Mean combined GHG flux expressed in CO<sub>2</sub> equivalents suggests a summer-season GHG sink in all treatments except for the early grazing treatment (figure 2(a)). In the early grazing treatment, mean flux of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O all were net emissions under ambient growing season conditions (figure 2(b)). In contrast, combined GHG flux in CO<sub>2</sub> equivalents from the late and no grazing treatments indicates a net sink because the large CO<sub>2</sub> uptake outweighs CH<sub>4</sub> emissions even

**Table 2.** Top performing models for greenhouse gas exchange based on AIC. Abbreviations: photosynthetically active radiation (PAR); air temperature (Air T); soil temperature at 10 cm (soil T); Stem height (Stem ht).

<i>Ecosystem Respiration Model</i>	LogLik	AIC	delta AIC	conditional pseudo $R^2$
Biomass + Grazing	-1152.6	2321.1	0	0.68
Biomass + Air T	-1163.4	2338.8	17.7	0.65
Biomass + Air T + Biomass*Air T	-1163.4	2340.8	19.7	0.66
Biomass + PAR	-1172.3	2356.5	35.4	0.65
<i>Gross Primary Productivity Model</i>	LogLik	AIC	delta AIC	conditional pseudo $R^2$
Biomass + PAR + Biomass*PAR	-1605.1	3224.2	0	0.60
Biomass + PAR	-1615.0	3242.0	17.8	0.59
Biomass + Grazing	-1623.5	3263.0	38.8	0.54
Stem ht + PAR + Stem ht*PAR	-1636.9	3287.9	63.7	0.55
<i>Net Ecosystem Exchange Model</i>	LogLik	AIC	delta AIC	conditional pseudo $R^2$
Stem ht + PAR + Stem ht*PAR	-1659.4	3332.7	0	0.51
Biomass + PAR + Biomass*PAR	-1661.0	3335.9	3.2	0.52
Biomass + Grazing	-1667.7	3351.5	18.8	0.44
Biomass + PAR	-1670.8	3353.7	21.0	0.50
<i>Methane Model</i>	LogLik	AIC	delta AIC	conditional pseudo $R^2$
Biomass + Grazing	-370.7	757.3	0	0.74
Stem ht + Grazing	-401.0	818.0	60.7	0.66
Biomass + PAR + Biomass*PAR	-413.5	841.0	83.7	0.54
Biomass + PAR	-416.0	843.9	86.6	0.53
<i>Nitrous Oxide Model</i>	LogLik	AIC	delta AIC	conditional pseudo $R^2$
Biomass + Soil T + Biomass*Soil T	-226.8	467.6	0	0.08
Biomass	-229.9	469.8	2.2	0.06
Biomass + Air T	-229.1	470.2	2.6	0.07
Stem ht + Soil T + Stem ht*Soil T	-228.3	470.5	2.9	0.07

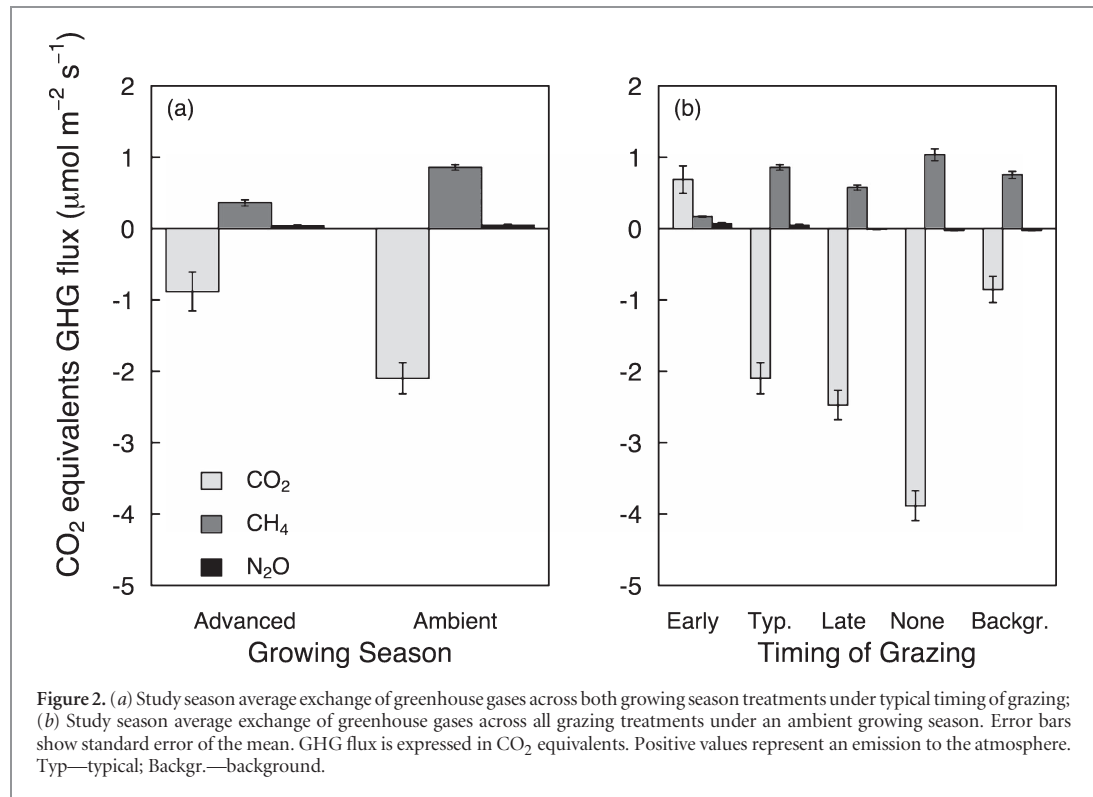
despite the greater global warming potential of  $\text{CH}_4$ . We also found a net sink in mean combined GHG flux of both the advanced and ambient growing season treatments (figure 2(a)). Throughout the study, the direction of the combined GHG flux was dominated by  $\text{CO}_2$ , with  $\text{CH}_4$  as the second most influential gas in all treatments. Despite its high global warming potential,  $\text{N}_2\text{O}$  emissions were so small that  $\text{N}_2\text{O}$  does not contribute noticeably to combined GHG flux.

## Discussion

Climate change is resulting in phenological mismatch between herbivores and their forage throughout a range of terrestrial environments (Lane *et al* 2012, Brook *et al* 2015, Middleton *et al* 2013, but see Gustine *et al* 2017). Rapidly warming temperatures at high latitudes may make these regions particularly prone to phenological mismatch. While previous studies have shown the effects of these mismatches on herbivore populations (Clausen and Clausen 2013, Doiron *et al* 2015), our study demonstrates that mismatches can also alter GHG emissions in the summer breeding areas of migratory species. More specifically, we found that functionally late grazing can decrease summer-season GHG emissions primarily through greater  $\text{CO}_2$  uptake (figure 2). In contrast, early grazing relative to the growing season results in emissions of both  $\text{CH}_4$

and  $\text{CO}_2$ . In all treatments except early goose grazing, GHG exchange was determined by opposing forcing of  $\text{CO}_2$  and  $\text{CH}_4$  fluxes, which acted as a sink and a source respectively. These results suggest that the developing phenological mismatch in coastal western Alaska, in which geese are arriving into a more phenologically advanced system, may result in increased GHG uptake during the summer season.

Rates of GHG exchange observed in our study are comparable, or slightly lower, than rates observed in similar high latitude ecosystems (Bartlett *et al* 1992, Kelsey *et al* 2016, Sturtevant and Oechel 2013). The overall exchange of GHG in this ecosystem was dominated by  $\text{CO}_2$  flux, followed by  $\text{CH}_4$  flux, with little contribution from  $\text{N}_2\text{O}$  emissions (figures 2 and 3). We found that  $\text{CO}_2$  exchange contributed between 50 and 80% of the combined GHG flux expressed in  $\text{CO}_2$  equivalents (figure 2), and was controlled primarily by vegetation height and an interaction between vegetation height and PAR (table 2). While we are not aware of any existing studies that examine the effects of changes in the timing of grazing on  $\text{CO}_2$  exchange, previous studies on the effect of grazing exclusion indicate that herbivory influences  $\text{CO}_2$  exchange through herbivory-induced changes to primary productivity and local soil environment (Cahoon *et al* 2012, Gornall *et al* 2009, Falk *et al* 2015, Sjögersten *et al* 2011). Our results suggest that in addition to herbivore exclusion, timing of herbivory is also an important



driver of CO<sub>2</sub> exchange through a similar mechanism, specifically that early grazing reduces CO<sub>2</sub> uptake by reducing primary productivity, while late grazing increases CO<sub>2</sub> uptake by increasing primary productivity. It is also likely that the duration of herbivory, in addition to timing, influences final GHG balance.

CH<sub>4</sub> was the second largest contributor to total GHG emissions and acted as a GHG source in all treatments (figures 2 and 3). Our results underscore the importance of the timing of grazing as a driver of CH<sub>4</sub> emissions (table 2) and suggest that delaying grazing contributes to greater CH<sub>4</sub> emissions through vegetation-induced increases in CH<sub>4</sub> production. The soil of northern wetlands is often O<sub>2</sub> poor, and vegetation can fuel CH<sub>4</sub> oxidation by transporting O<sub>2</sub> to the rhizosphere during photosynthesis (Ding *et al* 2005, Caffrey and Kemp 1991), or can stimulate methanogenesis through the production of photosynthetically-derived root exudates (Whiting and Chanton 1992, Shannon *et al* 1996, Lai *et al* 2014). Grazing is also known to stimulate root exudation of carbon (Hamilton and Frank 2001, Bardgett *et al* 1998) which affects soil biota and ecosystem function (Bardgett and Wardle 2003). Both of these processes may be relevant in this region because our modeling indicates biomass and timing of grazing are the most important controls on CH<sub>4</sub> emissions in this study (table 2) and specifically that greater GPP in late grazing and no grazing treatments increases CH<sub>4</sub> emissions to the atmosphere (figures 1 and 3).

N<sub>2</sub>O emissions did not contribute to total GHG forcing, with the exception of small emissions in the

early grazing treatment (figures 2 and 3). N<sub>2</sub>O flux was controlled weakly by soil temperature, biomass, and their interaction indicating that de-vegetated plots have higher N<sub>2</sub>O flux, especially at higher soil temperature (table 2). Although the relationship is not strong, this finding is consistent with previous research, which suggests that plants at this site may directly take up amino acids, particularly because N is important for osmotic regulation of the salt-tolerant *Carex* species present at this study site (Ruess *et al* 1997). If direct uptake of amino acids by plants limits N mineralization, then denitrification may be substrate-limited, thus decreasing N<sub>2</sub>O emissions in areas with greater primary productivity and increasing flux in areas with lower primary productivity. However, without large increases in soil temperature, N<sub>2</sub>O emissions from this ecosystem will likely remain inconsequential and phenology-induced changes in GHG exchanges in this system will come from CO<sub>2</sub> and CH<sub>4</sub>.

The developing phenological mismatch explored here is an important component of on-going change in GHG exchange in this region in response to changing climate. Even though grazing lawns compose only about 10% of the landscape in this region, they are the only portion of the landscape with appreciable CH<sub>4</sub> emissions (Kelsey *et al* 2016) and are also the vegetation community expected to experience the largest increase in GHG emission with a warming or advancing growing season (Kelsey *et al* 2016). Our results indicate that for the experimental treatments imposed here, changes in timing of grazing have a greater effect than season advancement, highlighting the importance of

timing of grazing for determining GHG flux in this region. The climatic changes that result in phenological mismatch will also likely affect other components of the ecosystem such as soil moisture and water table depth, and while extreme soil drying in this region could limit soil respiration and CH<sub>4</sub> emissions, due to the wet nature of this coastal system it is unlikely that soil moisture will become limiting in the near future.

Our study has a few limitations that constrain our results, but do not alter our conclusions. First, like all experimental studies, our results are constrained by the experimental treatments imposed. Our experiment explored only one scenario of advanced growing season (ca. 21 days), and it is possible that stronger or earlier warming could result in larger growing season effects on GHG exchange. Similarly, a phenological mismatch of less than 21 days could result in smaller effects on GHG exchange. In either case the nature of the change may affect the strength of the GHG response, but not the direction (sink versus source). Second, the logistical constraints associated with our remote study site limited the temporal resolution of our flux measurements to approximately two measurements per week, thus we report seasonal mean GHG emissions rather than a season-long cumulative GHG balance. However, we are confident our study design is sufficient to characterize the direction of summer season GHG exchange in this ecosystem for several reasons. First, the largest contributor to GHG exchange at this site is CO<sub>2</sub> which is also generally less spatially and temporally variable than CH<sub>4</sub> and N<sub>2</sub>O (Dai *et al* 2012). While CH<sub>4</sub> exchange has the potential to be more spatially and temporally variable than CO<sub>2</sub>, it is clear that the frequency of our observations allowed us to account for large variability in CH<sub>4</sub> fluxes (supplemental figure 5). Finally, N<sub>2</sub>O fluxes at this site are so small that they are essentially zero, and therefore these fluxes do not affect net GHG balance.

In high latitude regions, temperatures are projected to continue increasing at a faster rate than the rest of the globe with increases up to 5° C by 2100 (Myhre *et al* 2013), and this trend will likely further exacerbate phenological mismatch in this region (Clausen and Clausen 2013). Our results suggest that phenological mismatch, particularly a change in the timing of grazing, is important for future GHG emissions in high latitude wetland ecosystems which cover ~346 Mha in the northern hemisphere. Increasing the strength of the phenological mismatch already developing between brant and their forage in western Alaska will likely increase the summer-season GHG sink by promoting primary productivity that will override the concurrent increase in CH<sub>4</sub> emissions. However, it is also possible that changing migration patterns of brant in this region, such as the increasing percent of brant overwintering further north (Ward *et al* 2009), could prompt geese to arrive earlier in the Y-K Delta relative to the growing season and switch the

summer-season GHG flux from negative to positive. Finally, the largest changes to GHG emissions at this site would occur if this ecosystem was not grazed. Researchers have identified long-term declines in brant population at this site (Leach *et al* 2017), and some have hypothesized that the populations may decrease on the Y-K Delta while increasing in other areas, such as the North Slope of Alaska where they also breed and molt, if forage quality becomes more beneficial elsewhere (Flint *et al* 2008, Tape *et al* 2013). This scenario would increase CH<sub>4</sub> emissions, but also CO<sub>2</sub> uptake, and ultimately result in the most substantial increase in summer season average GHG uptake. Taken together our results suggest that projections of the role of arctic and subarctic ecosystems in the global climate system should account for climate-driven changes in grazing phenology to characterize how emissions and the source/sink status of these ecosystems will change under future climate conditions.

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