



## Observations of late-winter marine productivity in an ice-covered fjord, West Greenland

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**Abstract.** Direct observations of marine microbial metabolism are sparse in the Arctic, particularly under sea ice during winter. This paper presents the first observations of Arctic winter microbial activity under sea ice in a west Greenland fjord  
10 (Lillefjord, ~70° N). Here, measured changes in dissolved oxygen (DO) content in light and dark in-situ incubations were used to calculate net community productivity, respiration and photosynthesis rates. Data were collected at two fully ice-covered sites during February 2013, shortly after the end of the polar night. Averaged over the full study period, dark incubations showed statistically significant decreases in DO of  $-0.36 \pm 0.24$  (near shore) and  $-0.09 \pm 0.07$   $\text{gO}_2 \text{ m}^{-3} \text{ d}^{-1}$  (fjord centre), which are 2-20 times greater than rates previously reported under sea ice in the Arctic. The data provide no  
15 significant evidence for photosynthesis or any temporal change in metabolism rates over the study period; however, ambient sea water DO increased significantly at the fjord centre ( $0.023 \pm 0.013$   $\text{gO}_2 \text{ m}^{-3} \text{ d}^{-1}$ ), possibly attributable to sea ice algal photosynthesis. These incubation data may improve our understanding of microbial activity in the fjord during winter, and their contribution to Arctic ecosystems under present and future conditions. The data are archived at PANGAEA (<https://doi.pangaea.de/10.1594/PANGAEA.906332>, Chandler and Mackie, 2019).

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## 1 Introduction

There is increasing evidence for rapid climate change in the Arctic, with wide-reaching impacts in both terrestrial and marine environments (Wassman et al., 2011; McMeans et al., 2013; Post et al., 2013; Comiso and Hall, 2014). The observed reduction in sea ice cover (duration, extent and/or thickness), and the corresponding increase in solar illumination in the upper layers of the Arctic Ocean is of particular interest. While estimates of marine net primary productivity (NPP) based on satellite retrievals of chlorophyll *a* have shown a link between reductions in sea ice cover and increases in NPP across much of the Arctic during 1998-2009, details of the processes associated with this change and its effects on higher levels of the food chain remain uncertain (Hansen et al., 2003; Arrigo et al., 2008; Brown and Arrigo, 2012; Vancoppenolle et al., 2013).

The logistical challenges associated with making direct observations of Arctic marine microbial metabolism mean that very few field data are available with which to assess metabolism magnitudes and controlling factors (Matrai et al., 2013; Vaquer-Sunyer et al., 2013). Satellite retrievals of chlorophyll *a* can provide excellent temporal and spatial coverage for monitoring NPP, but have significant limitations. The data processing algorithms depend on multiple assumptions that may not be justified or appropriate in all cases (Arrigo et al., 2008); for example there may not be a direct relationship between retrieved chlorophyll *a* concentration and NPP (Flynn et al., 2013); data are unavailable for ocean water under sea ice and for sea ice itself, where productivity can be significant (Gosselin et al., 1997). Furthermore, the spatial resolution is generally too coarse to resolve smaller scale features such as fjords, where the combination of nutrient inputs and buoyant mixing driven by subglacial melt-water discharge from marine-terminating glaciers can stimulate particularly high levels of productivity (Meire et al., 2017). Field observations of biological processes are therefore extremely valuable, both for improving and validating the parameterisations used in satellite retrieval algorithms, and for providing information that cannot be measured remotely (e.g. in regions too small to be resolved by current remote sensing methods; or for observing individual components of microbial metabolism; variability with depth).

Two approaches are generally followed for quantifying microbial metabolism: first, measuring the dissolved oxygen (DO) content of sea water in-situ (Pomeroy, 1997; Rysgaard et al., 2001; Sherr and Sherr, 2003); or second, measuring changes in the concentration of chemical tracers in closed incubation experiments. The former method enables observations at high spatial and/or temporal resolution, but their interpretation is often challenging because the system is open: changes in oxygen concentration due to biological activity must be separated from those of physical processes such as mixing and air-water gas exchange. Monitoring ambient DO in this way only quantifies net community productivity (NCP). In the latter technique, changes in DO or radioisotope concentrations can be used to infer rates of biological processes (Smith, 1994, 1995; Gosselin et al., 1997; Rysgaard et al., 1999, 2001; Hill and Cota, 2005; Regaudie-de-Gioux and Duarte, 2010; Vaquer-Sunyer et al., 2013). This requires samples to be collected and incubated, potentially involving complex analytical procedures, and while in-situ incubations are unlikely to fully replicate natural conditions, they allow for more controlled conditions. Comparison of simultaneous incubations of samples exposed to light and samples kept in the dark yields estimates of community respiration (CR, measured in the dark samples) and gross primary productivity (GPP, interpreted as the difference between the light and dark samples) in addition to NCP (light samples). Ideally, the two approaches are used in tandem (Sherr and Sherr, 2003; Cottrell et al., 2006).

Observations based on the above field methods have shown that several physical factors, notably dissolved nutrients and irradiance, as well as biological factors such as species composition and abundance, are each likely to play important roles in different environments and seasons, leading to a diverse range of measured metabolism rates (see Table 1 in this paper and Table 3 in Vaquer-Sunyer et al., 2013). The contribution of sea ice algae to the Arctic Ocean's annual primary production has also been observed to vary widely, for example ranging from 2-57 % (mean 17 %) in summer 1994 (Gosselin et al.,



1997), to less than 1 % in Young Sound (NE Greenland) in summer 2000 (Rysgaard et al., 2001). The different methods and  
65 sampling strategies that are implemented by different teams make like-for-like comparison of observational data difficult.  
Despite both this and the high variability of the measured processes, some patterns have emerged. Notably, so-called blooms  
have been observed at, or shortly after, the break-up of the sea ice in summer, when microbial populations, chlorophyll *a*  
concentrations and microbial metabolism (both GPP and CR) in the surface layers are seen to increase rapidly (Sherr et al.,  
2003; Belzille et al., 2008; Mikkelsen et al., 2008; Terrado et al., 2008; Vaquer-Sunyer et al., 2013).

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While most measurements of metabolism have been carried out in ice-free summer conditions, there is evidence that  
microbial populations persist in both the sea ice and surface waters throughout the polar night (Berge et al., 2015; Vader et  
al., 2015) and can respond within a few days to increases in illumination (Zhang et al, 1998). Metabolism measurements in  
the water column under continuous sea ice, of which there are very few (Table 1), have detected community respiration  
75 during the polar night (Sherr and Sherr, 2003) but have yielded mixed results (positive, negative and insignificant NCP)  
during spring and summer (Gosselin et al., 1997; Cottrell et al., 2006, Seuthe et al., 2011; Vacquer-Sunyer et al., 2013). In  
Franklin Bay (70° N), chlorophyll *a* concentrations in sea-ice algae and in the upper 11 m of the water column started to  
increase in mid-February, despite the persistence of continuous sea ice cover up to 2 m thick (Belzille et al., 2008),  
demonstrating how increasing activity by primary producers sometimes begins even under thick ice as daylight returns, well  
80 before ice break-up.

Models have predicted a strong ecological response to changing sea ice conditions along Greenland's west coast (Hansen et  
al., 2003), yet there are very few direct observations from the fjords that dominate Greenland's coastline (Rysgaard et al.,  
1999, 2001; Mikkelsen et al., 2008; Matrai et al., 2013). Although only accounting for a small fraction of the total sea  
85 surface area in the Arctic, fjord waters have the potential to make a disproportionately strong contribution to Arctic marine  
productivity. This is partly due to the extensive area of shallow water along the long fjord coastlines, where benthic  
production can be important (Glud et al., 2002; Attard et al., 2014), and partly to the large nutrient fluxes transported to the  
fjords in melt water runoff from the Greenland Ice Sheet (Hawkings et al., 2014; Lawson et al., 2014; Meire et al., 2017).

90 There is a need for more observations of microbial metabolism in Greenland's fjords and under sea ice. Such measurements  
will allow us to better understand marine productivity, and quantify its contribution to Arctic marine ecosystems. Here we  
present in-situ observations of microbial metabolism made under continuous sea ice cover at ~70° N in a west Greenland  
fjord (Lillefjord), derived from changes in DO measured in incubation experiments and in ambient sea water during  
February-March 2013, shortly after the transition from polar night to spring conditions.

## 95 **2 Field Site and Methods**

Measurements were made in Lillefjord, West Greenland (70° 30' N, 50° 40' W). Lillefjord is 16 km-long branch of the  
Uummannaq Fjord system, which opens to Baffin Bay approximately 70 km from the field site. The fjord system (including  
Lillefjord itself) receives melt water runoff and calving icebergs from several outlet glaciers that drain the Greenland Ice  
Sheet, in common with many similar fjords in Greenland. In the winter of 2012/2013, continuous sea ice in Lillefjord had  
100 not formed until late January, which, although similar to several immediately preceding winters, was considered locally to be  
unusually late (fishermen in Uummannaq Fjord, pers. comm.).

Data were collected at two sites approximately mid-way between the calving front at the head of Lillefjord and the  
confluence of Lillefjord with Uummannaq Fjord (Fig 1). Hole 1 (fjord edge) was approximately 50 m from the shore, in



105 water 5-10 m deep; Hole 2 (fjord centre) was located centrally in the fjord in water ~300 m deep (N. Chauché, S. V. Gambo,  
pers. comm.). The sea ice thickness was initially measured as approximately 27 cm at both sites and increased slightly (by  
less than 10 cm) during the study period. Snow was absent from the sea ice until 13 February, then present in variable  
amounts thereafter (changes in these conditions are reported in Table 2).

110 Rates of photosynthesis and respiration were quantified using in-situ incubation experiments in the uppermost ~30 cm of the  
water column under the sea ice, based on measured changes in the DO content of sea water samples. A total of 13  
experiments were carried out between 6 February and 6 March 2013. In each experiment, up to ten samples of sea water  
were collected and incubated in-situ under the sea ice in 250 ml biological oxygen demand (BOD) bottles. Half the bottles  
were wrapped in tin foil to make them opaque to light (dark bottles) and the remainder were left unwrapped and transparent  
115 to light (light bottles). It was assumed that no photosynthesis took place in the dark bottles, so any changes in DO between  
the start and end of the experiment ( $\Delta DO_{\text{dark}}$ ) are attributed solely to community respiration (CR). Both respiration and  
photosynthesis can occur in light bottles, so the change in DO ( $\Delta DO_{\text{light}}$ ) is assumed to indicate net community production  
(NCP). Rates of gross primary productivity (GPP), inferred to be photosynthesis, are estimated using the difference in  $\Delta DO$   
between the light and dark bottles, i.e.  $NCP - CR$ . This is a standard and well-established method for measuring rates of  
120 microbial metabolism in fresh-water and marine ecosystems (Sherr and Sherr, 2003; Cottrell et al., 2006; Vaquer-Sunyer et  
al., 2013).

To begin each experiment, a hole of approximately 30 cm diameter was cut in the sea ice, using hand tools to avoid oil  
contamination. Water salinity and temperature were measured using a WTW handheld electrical conductivity (EC) meter  
125 (manufacturer's stated accuracy: temperature  $\pm 0.1^\circ \text{C}$ ; EC  $\pm 0.5\%$ ), and the approximate ice thickness and overlying  
undisturbed snow depth were measured using a ruler. Both the ice thickness and snow depth were disturbed by the opening  
and reopening of the hole, so the measurements made at the start of each experiment should only be interpreted as indicative  
of the general ambient conditions. A metal sieve was used throughout sample collection to remove ice debris from the water  
surface in the hole, to prevent ice fragments from entering the sample bottles. Due to the typically cold air temperatures ( $-25$   
130 to  $-5^\circ \text{C}$ ), the bottles were kept warm before use by adding ~20 ml of boiling sea water to each bottle prior to transport to the  
field site; the bottles were then kept in an insulated box until needed. This was important to avoid the sea water freezing  
directly onto the cold glass, which could have caused formation of ice inside the bottle or compromised the seal around the  
stopper. Immediately prior to sampling, each bottle was rinsed three times with sea water taken from the hole. The bottles  
were then refilled with water from the hole and suspended just under the water surface (to prevent ice from forming on the  
135 inside of the bottle). The water temperature and DO content in the bottle were measured using a PreSens Fibox3 fibreoptic  
oxygen meter (manufacturer's stated accuracy:  $\pm 1\%$ ), which outputs data every 1 s. To measure the DO in each bottle, the  
sensor was allowed to stabilise (normally within 60 s), and readings were then taken for a further 20 s. The mean of these  
readings was recorded as the initial DO for the sample. After making the measurements, the bottle was immediately sealed  
with a glass stopper. The stoppers are buoyant, so a small piece of tin foil was wrapped over the stopper to keep it in place.  
140 The Fibox3 sensor control unit often stops functioning at cold temperatures, so it was kept warm in the insulated box with  
the preheated bottles. Bottles were checked carefully once filled and sealed to ensure that no air bubbles were present. They  
were then left suspended on nylon ropes approximately 50 cm below the ice surface. Bottles were left in place for periods of  
24-96 hours. After the allocated time, the hole was carefully reopened and the bottles retrieved and transferred to an  
insulated box for transport back to the field base. It was not practical to make the final DO measurements at the incubation  
145 site because, after being removed from the sea, the water in the bottles would have started to freeze in the time taken to  
record the measurements. Therefore, the sealed bottles were transported in an insulated carrier to the field base, where the  
final DO and temperature were measured using the same Fibox3 sensor and probe. As for the initial DO measurements, the



mean of readings made for 20 s after the sensor had stabilised were recorded as the final DO for the sample. The time between extraction from the hole and DO measurement was approximately one hour, and temperature data showed the water temperature in the bottles to have increased by less than 2° C between removal from the incubation site and completion of the of the last measurement at the field base.

The main problems encountered during sample installation and recovery were associated with the cold air temperatures, which sometimes caused equipment failure (Fibox system and/or netbook) or caused ice crystals to form in bottles. On 8<sup>th</sup> February we were interrupted when filling the bottles, by a calving event which threatened to cause break-up of the sea ice. Therefore, we were not always able to obtain results from the full set of 10 bottles (as indicated by  $N_L$  and  $N_D$  in Table 2).

When converting between oxygen demand and carbon storage in Table 1, a 1:1 stoichiometric ratio between CO<sub>2</sub> and O<sub>2</sub> was used, although this ratio is noted to be subject to some uncertainty (Telling et al., 2010). We note that interpretation of the measurements would benefit from simultaneous measurements of microbial biomass; however, facilities for measuring biomass were not available at the field site.

## 2.1 Uncertainty Calculations

After each experiment, the difference between initial and final DO was calculated for each bottle, and the mean ( $\mu$ ) and standard deviation ( $\sigma$ ) of the differences were used to infer the change in DO ( $\Delta DO$ ). The number of bottles ( $n$ ) in any one experiment was small, so it is appropriate to use a t-distribution when calculating the 95 % confidence interval for  $\Delta DO$ . Treating light and dark bottles separately,  $\Delta DO$  was divided by the incubation time ( $T$ ) to give the rate of change in DO,  $\Delta DO / T$  as shown in (1), where  $t$  is the critical value of the t-distribution at the 95 % confidence level.

$$\Delta DO / T = [ \mu \pm t\sigma(n-1)^{-0.5} ] / T \quad (1)$$

The confidence intervals for  $\Delta DO_{\text{light}}$  and  $\Delta DO_{\text{dark}}$  were propagated through the calculations for rates of NCP, CR and photosynthesis. Each of these rates is therefore reported with an uncertainty corresponding to the limits of the 95 % confidence interval, and is considered significant if zero lies outwith the interval.

The mean and standard deviation of the initial DO measured in all the bottles (light and dark) were used to quantify the ambient DO and associated 95 % confidence interval for the sea water at each experiment start time, again using the t-distribution as in (1). A linear fit was then applied to the time series of ambient DO at each study site, using linear least-squares regression. The gradient of the fit represents the mean rate of change in ambient DO over the study period, and is reported with the 95 % confidence interval calculated using the  $t$  distribution and regression parameters.

## 3 Results

Throughout the study period, the sea water temperature and salinity varied between -1.5 and -1.7° C, and between 32.6 and 32.8 psu, respectively (Fig. 2a). The mean  $\pm 1\sigma$  DO of ambient seawater was  $12.24 \pm 0.23 \text{ gO}_2 \text{ m}^{-3}$  (fjord edge) and  $12.38 \pm 0.20 \text{ gO}_2 \text{ m}^{-3}$  (fjord centre). Linear regression analysis yielded no significant change in DO with time during the study period at the fjord edge ( $-0.001 \pm 0.031 \text{ gO}_2 \text{ m}^{-3} \text{ d}^{-1}$ ), while at the fjord centre there was a statistically significant increase in DO at a rate of  $0.023 \pm 0.013 \text{ gO}_2 \text{ m}^{-3} \text{ d}^{-1}$ , equivalent to  $720 \pm 410 \text{ nM O}_2 \text{ d}^{-1}$ .



For each incubation experiment, the changes in DO ( $\Delta DO$ ) measured for each of the individual light and dark bottles were averaged to give a mean  $\Delta DO_{\text{light}}$  and  $\Delta DO_{\text{dark}}$  for the experiment. For 3 out of the 5 incubation experiments at the fjord edge, and 3 out of the 8 experiments at the fjord centre,  $\Delta DO_{\text{light}}$  showed a significant decrease (Table 2, Fig 2b).  $\Delta DO_{\text{dark}}$  showed a significant decrease for 2 out of 4 experiments at the fjord edge, and for 2 out of 7 experiments at the fjord centre.

Results for all the bottles in all the incubations were grouped together (averaging the rates of change in DO for all light bottles and all dark bottles separately), to reflect mean conditions over the whole study period. This was done separately for the two study sites. We found a significant decrease in DO for the dark bottles at the fjord edge, and for both the light and dark bottles at the fjord centre ( $-0.36 \pm 0.24 \text{ gO}_2 \text{ m}^{-3} \text{ d}^{-1}$  for dark bottles at the fjord edge;  $-0.10 \pm 0.07$  and  $-0.09 \pm 0.07 \text{ gO}_2 \text{ m}^{-3} \text{ d}^{-1}$  for light and dark bottles at the fjord centre, respectively). There was no significant change in DO for light bottles at the fjord edge.

For each incubation experiment, the difference between  $\Delta DO$  calculated for the light and for the dark bottles is interpreted as GPP. None were found to be significantly different from zero (Fig. 2d) except for the first experiment at the fjord edge, where the 95 % confidence interval for GPP was  $0.31 \pm 0.28 \text{ gO}_2 \text{ m}^{-3} \text{ d}^{-1}$ .

#### 4 Discussion

Significant decreases in DO in the dark incubations at both sites are attributed to microbial respiration (Fig. 2b and Table 2). This is consistent with the few previous observations of microbial metabolism under sea ice cover, which have found significant CR (Table 1), and is not unexpected given the persistence of microbial communities through the polar night (Berge et al., 2015); however, in Lillefjord the measured rates (particularly at the fjord edge) are considerably higher than those at other ice-covered sites (Table 1). In common with most previous studies (both open water and ice-covered, see Section 1 and Table 1), our observations have high variance.

The rate of change in DO in the light bottles is interpreted as NCP, which was either weakly negative or insignificant. These findings for NCP at Lillefjord are consistent with observations from the one other west Greenland fjord studied during February-March, to our knowledge (NCP  $< 0.001 \text{ gO}_2 \text{ m}^{-3} \text{ d}^{-1}$  at Kangerluarsunnguaq in sub-Arctic SW Greenland; Mikkelsen et al., 2008). They are also consistent with some studies of ice-covered open ocean sites (Sherr and Sherr, 2003; Hill and Cota, 2005), but contrast with others (weakly positive NCP was reported by Cottrell et al., 2006 in the Arctic Ocean and by Vaquer-Sunyer et al., 2013 in the Fram Strait). With the exception of Sherr and Sherr (2003), measurements at these ice-covered ocean sites were collected later in the year (mid-April to June) than those at Lillefjord.

The lack of any significant difference between  $\Delta DO$  in the light and dark bottles means that there was no significant evidence for GPP (or photosynthesis). This should not be interpreted as significant evidence for no photosynthesis, particularly given the high variance in the data indicated by wide 95 % confidence intervals; however, it does show that the rate of photosynthesis – if it was occurring – must have been much smaller than that of respiration. Rysgaard et al. (1999) and Mikkelsen et al. (2008) both found evidence for very low rates of photosynthesis under sea ice in fjords shortly before ice break-up (GPP  $< 0.003 \text{ gO}_2 \text{ m}^{-3} \text{ d}^{-1}$  in Young Sound, Rysgaard et al., 1999; NCP =  $+0.001 \text{ gO}_2 \text{ m}^{-3} \text{ d}^{-1}$  in Kangerluarsunnguaq, Mikkelsen et al., 2008). Other studies have found evidence for significant GPP in the largely (> 80 %) ice-covered open ocean in the Fram Strait during April-May, which contributed to an overall positive NCP (Seuthe et al., 2011; Vaquer-Sunyer et al., 2013). Under continuous first-year sea ice in Franklin Bay (a coastal site at a similar latitude to Lillefjord), Terrado et al. (2008) observed an increase in the abundance of photosynthetic organisms as early as February in



response to increasing surface irradiance. Similarly, chlorophyll *a* concentrations were observed to reach a minimum in  
230 January, and to begin increasing in February, within first-year sea ice in the open Arctic Ocean in the Canada Basin  
(Melnikov et al., 2002). In Lillefjord, photosynthetic activity in the surface waters may not have commenced during the  
study period, or it may have been masked by the stronger and highly variable respiration signal.

In contrast to the incubation results, there was a significant increase in ambient DO at the fjord centre of  $0.023 \pm 0.013 \text{ gO}_2$   
235  $\text{m}^{-3} \text{ d}^{-1}$ . This differs from the findings of Sherr and Sherr (2003), where a decrease was observed in ambient DO under sea  
ice during winter in the western Arctic Ocean. Lillefjord was completely ice covered during the study period, preventing any  
air-water gas exchange, and no decrease in DO was observed in the incubation experiments. Therefore, the increase in  
ambient DO may have been due to sea algal photosynthesis on the underside of the sea ice, although further data would be  
needed to confirm the presence of ice algae. Ice algal photosynthesis has been observed elsewhere under continuous sea ice  
240 cover in other Greenland fjords (Rysgaard et al., 2001; Mikkelsen et al., 2008). If this was indeed the cause of the increase in  
ambient DO at Lillefjord, then it is likely that ice algal photosynthesis commenced earlier than photosynthesis in the  
underlying water column. These contrasting results from simultaneous incubation and in-situ experiments demonstrate the  
advantage of using both closed and open techniques when there is continuous ice cover.

245 Despite the increasing surface irradiance (longer daylight hours and less shading by surrounding topography at higher solar  
elevations), the incubation experiments provide no evidence for temporal changes in metabolism rates. It is possible that  
some of the increase in incident radiation at the snow/ice surface did not reach the water below the ice because of increases  
in snow cover and ice thickness over this same period. Without under-ice irradiance measurements this is necessarily  
uncertain; however, the radiation intensity *S* reaching the water column (as a fraction of surface incident radiation intensity  
250  $S_0$ ) can be estimated using  $S/S_0 = (1 - \alpha) \exp(-k_s z_{s,i} - k_i z_{i,i})$ , where  $\alpha$  is the surface albedo, and  $z_{s,i}$  and  $k_{s,i}$  are the thicknesses  
and extinction coefficients for snow and ice, respectively. Assuming extinction coefficients of  $4.8 \text{ m}^{-1}$  and  $0.9 \text{ m}^{-1}$  for snow  
and sea ice, and albedos of 0.90 and 0.65 for fresh snow and sea ice (following Mikkelsen et al., 2008), the under-ice  
irradiance is estimated as 31 % of the surface irradiance before snowfall on 14 February and 11 % afterwards. Therefore,  
increases in surface irradiance in early February as experienced under the ice, could have been considerably reduced  
255 following snowfall in mid February.

## 5 Data availability

The data are archived at PANGEA (<https://doi.pangaea.de/10.1594/PANGAEA.906332>, Chandler and Mackie, 2019).

## 6 Conclusions

These data provide a first indication of winter microbial metabolism beneath sea ice in an Arctic fjord in west Greenland.  
260 Thirteen in-situ incubation experiments provide strong evidence for microbial respiration at rates 2-20 times higher than  
those reported under sea ice elsewhere in the Arctic. The high variance in the NCP and CR results (both between individual  
bottles in one experiment, and between incubations) is a common characteristic of marine microbial metabolism  
measurements under sea ice (Table 1) and presents a challenge to accurate calculation of GPP or temporal trends. This  
variance should be carefully accounted for when considering uncertainties associated with estimates of the regional-scale  
265 contributions of microbial activity, which are necessarily based on the limited data that are currently available. In future  
studies this could be addressed by increasing the number of bottles and/or conducting more frequent experiments, and by  
extending the study period to obtain a longer time series. Finally, the contrast between the increasing trend in ambient  
seawater DO and the net oxygen decrease in the incubation experiments highlights potential differences between controlled



and open experiments. In this study, the difference is most likely attributable to net production by sea ice algae (which would  
270 increase DO in the ambient sea water), contrasting with net respiration in the underlying water (which would decrease the  
DO in the closed incubations). This suggests an earlier onset of photosynthesis at the underside of the sea ice than in the  
underlying water.

#### Author contributions

Both authors contributed equally to data collection, data analysis and preparation of the manuscript.

#### 275 Competing interests

The authors declare no competing interests.

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#### References

- Arrigo, K. R., van Dijken, G., and Pabi, S.: Impact of a shrinking Arctic ice cover on marine primary production. *Geophys. Res. Lett.* 35(L19603), doi:10.1029/2008GL035028, 2008.
- Attard, K. M., Glud, R. N., McGinnis, D. F., and Rysgaard, S.: Seasonal rates of benthic primary production in a Greenland  
285 fjord measured by aquatic eddy correlation. *Limnol. Oceanogr.* doi:10.4319/lo.2014.59.5.1555, 2014.
- Belzille, C., Brugel, S., Nozais, C., Gratton, Y., and Demers, S.: Variations of the abundance and nucleic acid content of heterotrophic bacteria in Beaufort Shelf waters during winter and spring. *J. Marine Syst.* 74, 946-956, 2008.
- Berge, J. and 16 others: In the dark: A review of ecosystem processes during the polar night. *Prog. Oceanogr.* 139, 258-271, doi:10.1016/j.pocean.2015.08.005, 2015.
- 290 Brown, Z. W. and Arrigo, K. R.: Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean. *ICES J. Mar. Sci.* 69(7), 1180-1193, doi:10.1093/icesjms/fss113, 2012.
- Chandler, D. and Mackie, S.: Observations of winter marine productivity in an ice-covered fjord, West Greenland. *PANGAEA*, <https://doi.pangaea.de/10.1594/PANGAEA.906332>, 2019.
- Comiso, J. C. and Hall, D. K.: Climate trends in the Arctic as observed from space. *WIREs Clim. Change* 5, 389-409  
295 doi:10.1002/wcc.277, 2014.
- Cottrell, M. T., Malmstrom, R. R., Hill, V., Parker, A. E., and Kirchman, D. L.: The metabolic balance between autotrophy and heterotrophy in the western Arctic Ocean. *Deep Sea Res. I.* 53, 1831-1844, 2006.
- Flynn, K. J., Stoecker, D. K., Mitra, A., Raven, J. A., Glibert, P. M., Hansen, P. J., Granéli, E., and Burkholder, J. M.: Misuse of the phytoplankton–zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton  
300 functional types. *J. Plankton Res.* 35(1), 3-11, doi: 10.1093/plankt/fbs062, 2013.
- Glud, R. N., Kühl, M., Wenzhöfer, F., and Rysgaard, S.: Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance for ecosystem primary production. *Mar. Ecol. Prog. Ser.* 238, 15-29, 2002.



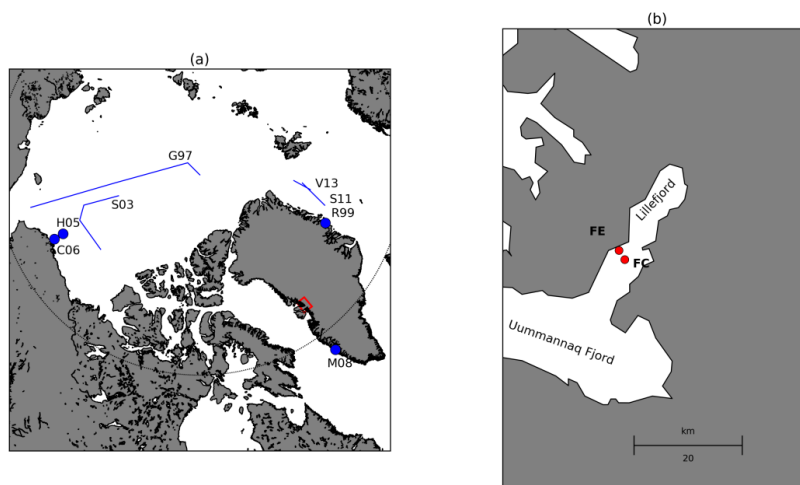


- Gosselin, M., Levasseur, M., Wheeler, P. A., Horner, R. A., and Booth, B. C.: New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep Sea Res. II*, 44, 1623-1644, 1997.
- 305 Hameedi, M. J.: Aspects of water column primary productivity during summer. *Mar. Biol.* 48, 37-46, 1978.
- Hansen, A. S., Nielsen, T. G., Levinson, H., Madsen, S. D., Thingstad, T. F., and Hansen, B. W.: Impact of changing ice cover on pelagic productivity and food web structure in Disko Bay, West Greenland: a dynamic model approach. *Deep Sea Res. I*, 50, 171-187, 2003.
- Harrison, W. G., Platt, T.: Photosynthesis-irradiation relationships in polar and temperate phytoplankton populations. *Pol. Biol.* 5, 153-164, 1986.
- 310 Hawkings, J. R., Wadham, J. L., Tranter, M., Raisewell, R., Benning, L. G., Stratham, P. J., Tedstone, A., Nieniow, P., Lee, K., and Telling, J.: Ice sheets as a significant source of highly reactive nanoparticulate iron to the oceans. *Nat. Commun.* 5, 3929, doi:10.1038/ncomms4929, 2014.
- Hill, V., Cota, G.: Spatial patterns of primary production on the shelf, slope and basin of the Western Arctic in 2002. *Deep Sea Res. II*, 52, 3344-3354, 2005.
- 315 Lawson, E. C., Wadham, J. L., Tranter, M., Stibal, M., Lis, G. P., Butler, C. E. H., Laybourn-Parry, J., Nienow, P., Chandler, D., Dewsbury, P.: Greenland Ice Sheet exports labile organic carbon to the Arctic oceans, *Biogeosciences*, doi:10.5194/bg-11-4015-2014, 2014.
- Matrai, P. A., Olson, E., Suttles, S., Hill, V., Codispoti, L. A., Light, B., and Steele, M.: Synthesis of primary production in the Arctic Ocean: I. Surface waters, 1954-2007.: *Prog. Oceanogr.* 110, 93-106, doi:10.1016/j.pocean.2012.11.004, 2013.
- 320 McMeans, B. C., Rooney, N., Arts, M. T., Fisk, A. T.: Food web structure of a coastal Arctic marine ecosystem and its implications for stability. *Mar. Ecol. Prog. Ser.* 482, 17-28, doi:10.3354/meps10278, 2013.
- Meire, L., Mortensen, J., Meire, P., Juul-Pedersen, T., Sejr, M. K., Rysgaard, S., Nygaard, R., Huybrechts, P., and Meysman, F. J. R.: Marine-terminating glaciers sustain high productivity in Greenland fjords. *Glob. Change Biol.* 23, 5344-5357, doi:10.1111/gcb.13801, 2017.
- 325 Melnikov, I. G., Kolosova, E. G., Welch, H., and Zhitina, L. S.: Sea ice biological communities and nutrient dynamics in the Canada Basin of the Arctic Ocean. *Deep Sea Res. I*, 49, 1623-1649, 2002.
- Mikkelsen, D. E., Rysgaard, S., and Glud, R. N.: Microalgal composition and primary production in Arctic sea ice: a seasonal study from Kobbefjord (Kangerluarsunnguaq), West Greenland. *Mar. Ecol. Prog. Ser.* 368, 65-74, doi:10.3354/meps07627, 2008.
- 330 Pomeroy, L.: Primary production in the Arctic Ocean estimated from dissolved oxygen. *J. Marine Syst.* 10: 1-8, 1997.
- Post, E., Bhatt, U. S., Bitz, C. M., Brodie, J. F., Fulton, T. L., Hebblethwaite, M., Kerby, J., Kutz, S. J., Stirling, I., and Walker, D. A.: Ecological consequences of sea ice decline, *Science* 341, 519-524, doi:10.1126/science.1235225, 2013.
- Regaudie-de-Gioux, A. and Duarte, C. M.: Plankton metabolism in the Greenland Sea during the polar summer of 2007. *Pol. Biol.* 33, 1651-1660, doi:10.1007/s00300-010-0792-1, 2010.
- 335 Rysgaard, S., Kühl, M., Glud, R. N., and Hansen, J. W.: Biomass, production and horizontal patchiness of sea ice algae in a high-Arctic fjord (Young Sound, NE Greenland). *Mar. Ecol. Prog. Ser.* 223: 15-26, 2001.
- Rysgaard, S., Nielsen, T. G., and Hansen, B. W.: Seasonal variation in nutrients, pelagic primary production and grazing in a high-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. *Mar. Ecol. Prog. Ser.* 179, 13-25, 1999.
- 340 Seuthe, L., Töpper, B., Reigstad, M., Thyrrhaug, R., and Vaquer-Sunyer, R.: Microbial communities and processes in ice-covered Arctic waters of the northwestern Fram Strait (75 to 80°N) during the vernal pre-bloom phase. *Aquat. Microb. Ecol.* 64, 253-266, doi:10.3354/ame01525, 2011.
- Sherr, B. F. and Sherr, E. B.: Community respiration/production and bacterial activity in the upper water column of the central Arctic Ocean. *Deep Sea Res. I*, 50, 529-542, 2003.



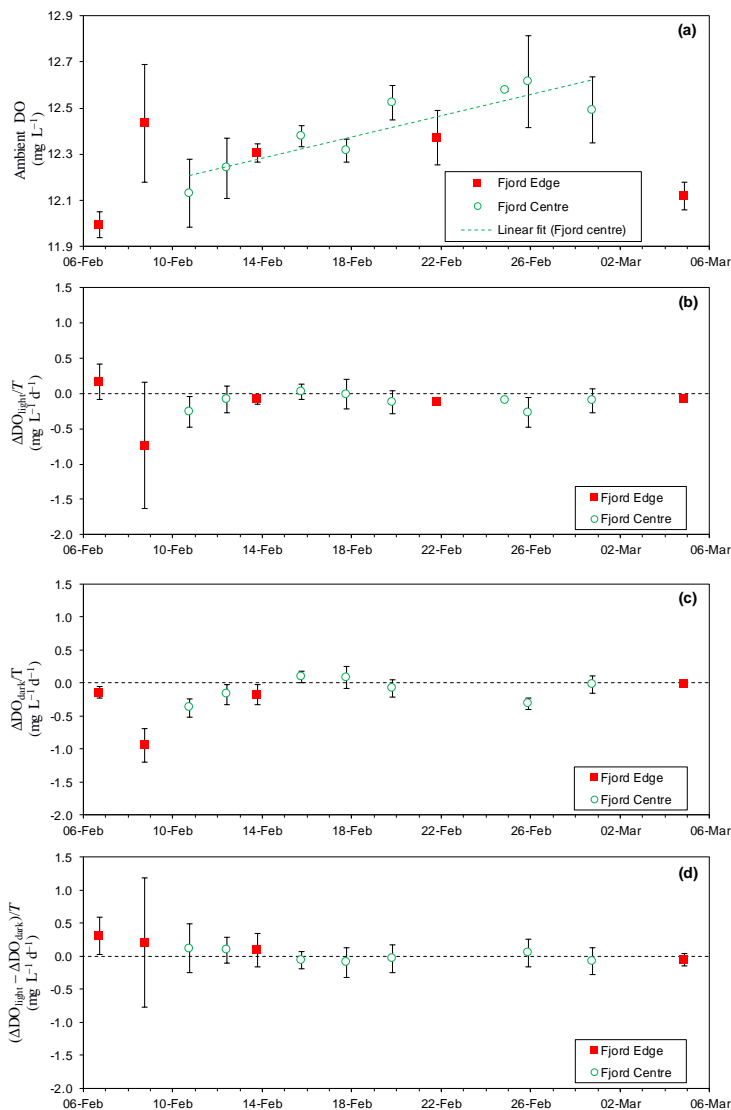
- 345 Sherr, E. B., Sherr, B. F., Wheeler, P. A., and Thompson, K.: Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. *Deep Sea Res. I.* 50, 557-571, 2003.
- Smith Jr., W. O.: Primary Productivity of a Phaeocystis Bloom in the Greenland Sea During Spring, 1989. *Geoph. Monog. Ser.* 85, 263-272, 1994.
- Smith Jr., W. O.: Primary productivity and new production in the Northeast Water (Greenland) Polynya during summer 1992.: *J. Geophys. Res.* 100(C3), 4357–4370, doi:10.1029/94JC02764, 1995.
- 350 Telling, J., Anesio, A. M., Hawkings, J., and Tranter, M.: Measuring rates of gross photosynthesis and net community production in cryoconite holes: a comparison of field methods. *Ann. Glaciol.* 51, 153-162, 2010.
- Terrado, R., Lovejoy, C., Massana, R., and Vincent, W.: Microbial food web responses to light and nutrients beneath the coastal Arctic Ocean sea ice during the winter–spring transition. *J. Marine Syst.* 74: 964-977, 2008.
- 355 Vader, A., Marquardt, M., Meshram, A. R., and Gabrielsen, T. M.: Key Arctic phototrophs are widespread in the polar night. *Pol. Biol.* 38, 13-21, doi:10.1007/s00300-014-1570-2, 2015.
- Vaquer-Sunyer, R., Duarte, C. M., Regaudie-de-Gioux, A., Holding, J. Garcia-Corral, L. S., Reigstad, M., and Wassmann, P.: Seasonal patterns in Arctic planktonic metabolism (Fram Strait – Svalbard region). *Biogeosciences* 10, 1451-1469, 2013, doi:10.5194/bg-10-1451-2013, 2013.
- 360 Vancoppenolle, M., Bopp, L., Madec, G., Dunne, J., Ilyina, T., Halloran, P. R., and Steiner, N.: Future Arctic Ocean primary productivity from CMIP5 simulations: Uncertain outcome, but consistent mechanisms. *Global Biogeochem. Cy.* 27, 605-619, doi:10.1002/gbc.20055, 2013.
- Wassmann P., Duarte, C. M., Agust, S., and Sejr, M. K.: Footprints of climate change in the Arctic marine ecosystem. *Glob. Change Biol.* 17, 1235-1249, doi:10.1111/j.1365-2486.2010.02311.x, 2011.
- 365 Zhang, Q., Gradinger, R., and Spindler, M.: Dark Survival of Marine Microalgae in the High Arctic (Greenland Sea). *Polarforschung* 65(3), 111-116, 1998.

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375 **Figure 1: (a) Locations where microbial metabolism has been measured in the water column under sea ice (minimum sea ice cover 80%). Abbreviations follow Table 1. Positions of points and transects are approximate, and are based on maps in the corresponding published works. The red box shows the location of Lillefjord, west Greenland. (b) Location of the fjord edge (FE) and fjord centre (FC) study sites.**

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**Figure 2:** Time series of (a) ambient DO concentration in the sea water at the start of each experiment; (b) rate of change of DO in the light incubation bottles ( $\Delta DO_{light}/T$ ), interpreted as the net community production rate (NCP); (c) rate of change of DO in the dark incubation bottles ( $\Delta DO_{dark}/T$ ), interpreted as the respiration rate (CR); (d) the difference ( $\Delta DO_{light} - \Delta DO_{dark}/T$ ), interpreted as the photosynthesis rate (GPP).

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**Table 1: Measurements of microbial metabolism under Arctic sea ice. Net Community Production (NCP) and Gross Primary Production (GPP) are positive if oxygen is being released. Community Respiration (CR) is positive if oxygen is being consumed. Abbreviations are as follows: inc: incubations using DO or <sup>14</sup>C; bd: below level of detection; NM: not measured; NR: measured, but not reported. Sources are: G97: Gosselin et al., 1997; R99 Rysgaard et al., 1999; S03 Sherr and Sherr, 2003; H05 Hill and Cota, 2005; C06 Cottrell et al., 2006; M08 Mikkelsen et al., 2008; S11 Seuthe et al., 2011; and V13 Vaquer-Sunyer et al., 2013. (a) Estimated from Fig. 2 in this paper. (b) Calculated using authors' range of 9.57 gC m<sup>-2</sup> d<sup>-1</sup> over estimated depth of 60 m, and reported as the mean ± 1 standard deviation of the values in Table 2 in this paper.**

LOCATION	DEPTH m	ICE COVER	METHOD	DATES	NCP gO <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup>	GPP gO <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup>	CR gO <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup>	REF
Arctic Ocean 75-90N Chukchi Sea to North Pole	0-60 <sup>(a)</sup>	>80 %	Inc ( <sup>14</sup> C), 12 hr, artificial light.	July-Aug 1994	NR	0.0004 to 0.0025 <sup>(b)</sup>	NR	G97
Young Sound, E Greenland 74N ~800 m from coast, in fjord Ice thickness decreasing from ~2m	0-35	100 %	Inc ( <sup>14</sup> C), 2 hr, artificial light.	June 1996	NR	<0.005	NR	R99
Central Arctic Ocean	0-50	100 %	Ambient DO	Nov-May 1997-8	-0.0025			S03
Chukchi Sea	0-~90	>80 %	Inc ( <sup>14</sup> C) artificial light	Spring 2002	<0.003	NM	NM	H05
Chukchi Sea	Surface 15% light 1% light	100 %	Inc (DO), dark, 72 hr	Autumn-winter 1997 Midwinter 1997-8	NM	NM	0.019 ± 0.014 0.008 ± 0.008 0.027 ± 0.019	
Kangerluarsunguaq, W Greenland, 64N, Fjord ~100m deep.	0-50		Inc ( <sup>14</sup> C), 2 hr, artificial light, 4°C.	May-June 2004	+0.07 ± 0.12 +0.22 ± 0.11 +0.08 ± 0.13	NM NM NM	0.17 ± 0.32 0.06 ± 0.01 0.08 ± 0.01	C06 <sup>(b)</sup> M08
Ice increasing 0-50 cm thickness Ice ~60 cm thickness		100 % 100 %		Dec Mar 2006-7 Apr 2007	<0.001 +0.001	NM NM	NM NM	
Fram Strait, 75-78N	0-20	>80 %	Inc (DO), 24 hr, in-situ.	Apr-May 2008			bd	S11
Site C1, 78N Site E, 75N					+0.056 -0.006		bd 0.031	
Fram Strait, 77-79N	0-20	'heavy'	Inc (DO), 24 hr in-situ	Apr 2007	+0.054 ± 0.027	+0.024 ± 0.012	0.025 ± 0.012	V13
Lillefjord, W Greenland, 70N Fjord edge	Surface	100 %	Inc (DO) in-situ. Ambient DO	Feb-Mar 2013	-0.17 ± 0.19 -0.001 ± 0.031	+0.19 ± 0.30	0.36 ± 0.24	This study
Fjord centre	Surface	100 %	Inc (DO) in-situ. Ambient DO		-0.10 ± 0.07 +0.023 ± 0.013	-0.01 ± 0.10	0.09 ± 0.07	



**Table 2** Summary of results obtained in the incubation experiments at the two holes FE (fjord edge) and FC (fjord centre). Quoted values are means with 95 % confidence intervals, except when N = 2 (as indicated by †), where the error bounds are simply the range of the two observations. T is the duration of the incubation, N is the number of samples, and L - D is the difference between the change in dissolved oxygen in the light bottles, and in the dark bottles ( $\Delta DO_{light} - \Delta DO_{dark}$ ).

Start time	Hole	T d	O <sub>2</sub> start gO <sub>2</sub> m <sup>-3</sup>	N <sub>L</sub> gO <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup>	ΔO <sub>2</sub> Light gO <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup>	N <sub>b</sub>	ΔO <sub>2</sub> Dark gO <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup>	L - D gO <sub>2</sub> m <sup>-3</sup> d <sup>-1</sup>	Notes
06 Feb 17:25	FE	1.0	12.00 ± 0.06	4	0.17 ± 0.24	4	-0.14 ± 0.14	0.31 ± 0.28	Cloudy throughout experiment.
08 Feb 17:57	FE	1.0	12.44 ± 0.25	4	-0.74 ± 0.90	4	-0.94 ± 0.40	0.21 ± 0.98	Cloudy throughout experiment. Calving event caused risk of ice breakup at experiment start, before all bottles filled.
13 Feb 18:30	FE	1.0	12.31 ± 0.04	5	-0.08 ± 0.07	4	-0.17 ± 0.24	0.09 ± 0.25	Clear at start but overcast by mid- morning of 14th and cloud steadily increased all day.
21 Feb 19:47	FE	4.0	12.37 ± 0.12 <sup>†</sup>	2	-0.12 ± 0.05 <sup>†</sup>	---	---	---	20-30 mm fresh snow. Clear sky.
04 Mar 20:45	FE	2.0	12.12 ± 0.06	3	-0.08 ± 0.03	2	-0.02 ± 0.10	-0.05 ± 0.10	Thin covering of wind scoured snow. Clear sky.
<b>Overall</b>	<b>FE</b>		<b>12.24 ± 0.08</b>	<b>18</b>	<b>-0.17 ± 0.19</b>	<b>14</b>	<b>-0.36 ± 0.24</b>	<b>0.19 ± 0.30</b>	
10 Feb 17:40	FC	1.1	12.13 ± 0.15	5	-0.26 ± 0.30	4	-0.38 ± 0.22	0.12 ± 0.37	Clear on 10th. Partly cloudy on 11th.
12 Feb 10:03	FC	1.0	12.24 ± 0.13	5	-0.08 ± 0.07	5	-0.17 ± 0.19	0.09 ± 0.20	Thin layer of snow. Clear morning on 12th, cloudy afternoon.
15 Feb 17:45	FC	1.0	12.38 ± 0.05	5	0.03 ± 0.08	5	0.09 ± 0.11	-0.06 ± 0.14	Thin layer of snow.
17 Feb 18:38	FC	1.1	12.32 ± 0.05	5	-0.01 ± 0.08	5	0.08 ± 0.21	-0.10 ± 0.22	5-10 mm fresh snow. Overcast on 17th. Cloudy but bright on 18th.
19 Feb 19:23	FC	1.1	12.52 ± 0.08	5	-0.12 ± 0.14	5	-0.08 ± 0.16	-0.04 ± 0.21	20-30 mm snow. High cloud and sunshine in morning of 20th, then increasing cloud.
24 Feb 20:36	FC	0.9	12.58 ± 0.01 <sup>†</sup>	2	-0.10 ± 0.03 <sup>†</sup>	---	---	---	30-30 mm snow. Clear sky.
25 Feb 21:29	FC	1.8	12.61 ± 0.20	2	-0.27 ± 0.03 <sup>†</sup>	3	-0.32 ± 0.21	0.05 ± 0.42	10-20 mm snow. Clear sky on 25th and 26th. Cloud increasing on 27th.
28 Feb 18:22	FC	2.1	12.49 ± 0.14	5	-0.10 ± 0.10	5	-0.03 ± 0.17	-0.08 ± 0.20	10-20 mm snow, partially melted on 28th. Overcast 28th February and 1st March, snow showers on 1st. Clear on 2 <sup>nd</sup> .
<b>Overall</b>	<b>FC</b>		<b>12.38 ± 0.05</b>	<b>34</b>	<b>-0.10 ± 0.07</b>	<b>32</b>	<b>-0.09 ± 0.07</b>	<b>-0.01 ± 0.10</b>	