Observations of late-winter marine ~~productivity~~microbial activity 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 (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 ± 0.24 (near shore) and -0.09 ± 0.07 gO_2 m^{-3} d^{-1} (fjord centre), ~~which are~~indicating respiration rates that were 2-20 times greater than rates previously reported under sea ice in the Arctic. Meanwhile, a lack of significant evidence for photosynthesis suggests that the rate of photosynthesis – if it was occurring – was much lower than that of respiration. The data ~~provide~~also show no significant evidence ~~for photosynthesis or any~~of a temporal ~~change~~trend in metabolism rates over the study period; however, ambient sea water DO increased significantly at the fjord centre (0.023 ± 0.013 gO_2 m^{-3} d^{-1}), possibly attributable to processes not occurring in the incubations (such as sea ice algal photosynthesis~~.~~). These ~~incubation~~ data may improve our understanding of microbial activity in the fjord during winter, and ~~their~~its contribution to Arctic ecosystems under present and future conditions. The data are archived at PANGEA (https://doi.pangaea.de/10.1594/PANGAEA.906332, Chandler and Mackie, 2019; https://doi.pangaea.de/10.1594/PANGAEA.912677, Chandler and Mackie, 2020).

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 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). A recent approach combined in-situ chlorophyll *a* and irradiance observations with a numerical model to estimate NPP under pack ice (Assmy et al., 2017); while less direct than ambient DO measurements or incubations, this method can yield good spatial coverage, is not affected by oxygen exchange with the atmosphere, and provides detailed in-situ observations that will help address the limitations of remotely-sensed chlorophyll *a* observations noted above.

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 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~~).~~; Assmy et al., 2017).

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 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 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 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).

There is a need for more observations of microbial metabolism in Greendland'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 on 21 January.

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

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 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).

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 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 (ΔDO_{dark}) are attributed solely to community respiration (CR). Both respiration and photosynthesis can occur in light bottles, so the change in DO (ΔDO_{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 ΔDO between the light and dark bottles, i.e. NCP – CR. This is a standard and well-established method for measuring rates of 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 (manufacturer's stated accuracy: temperature ± 0.1° C; EC ± 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 to -5° 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 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: ± 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. 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 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 8th 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).

Incubation times were initially chosen as 24 hrs, corresponding to one diurnal cycle. Since we were finding high variability in the early incubations, we also carried out some longer incubations (2 or 4 days) later in the study period. While these longer incubations allowed for potentially greater changes in DO (i.e., a lower signal to noise ratio), we also note that longer incubations increase the effects of methodological artefacts associated with the incubations being a closed rather than open system. We do not have enough data to confidently assess what the optimum incubation time would be.

When converting between oxygen demand and carbon storage in Table 1, a 1:1 stoichiometric ratio between CO_2 and O_2 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 (μ) and standard deviation (σ) of the differences were used to infer the change in DO (ΔDO). 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 ΔDO. Treating light and dark bottles separately, ΔDO 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.

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

The confidence intervals for ΔDO_{light} and ΔDO_{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 ± 1σ DO of ambient seawater was 12.24 ± 0.23 $gO_2\ m^{-3}$ (fjord edge) and 12.38 ± 0.20 $gO_2\ m^{-3}$ (fjord centre). Linear regression analysis yielded no significant change in DO with time during the study period at the fjord edge (-0.001 ± 0.031 $gO_2\ m^{-3}\ d^{-1}$), while at the fjord centre there was a statistically significant increase in DO at a rate of 0.023 ± 0.013 $gO_2\ m^{-3}\ d^{-1}$, equivalent to 720 ± 410 nM $O_2\ d^{-1}$~~.~~ (Fig. 2a).

For each incubation experiment, the changes in DO (ΔDO) measured for each of the individual light and dark bottles were averaged to give a mean ΔDO_{light} and ΔDO_{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, ΔDO_{light} showed a significant decrease (Table 2, Fig 2b). ΔDO_{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~~.~~ (Fig. 2c).

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 ± 0.24 $gO_2\ m^{-3}d^{-1}$ for dark bottles at the fjord edge; –0.10 ± 0.07 and –0.09 ± 0.07 $gO_2\ m^{-3}d^{-1}$ 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 ΔDO 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 ± 0.28 $gO_2\ m^{-3}d^{-1}$.

4 Discussion

Significant decreases in DO in the dark incubations at both sites are attributed to microbial respiration (Fig. ~~2b~~2c 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~~standard deviations.

The rate of change in DO in the light bottles ~~is interpreted as~~(considered to represent NCP~~, which~~) was either weakly negative or insignificant. These ~~findings~~results 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 $gO_2\ m^{-3}d^{-1}$ 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 ΔDO 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. For comparison, 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 $gO_2\,m^{-3}d^{-1}$ in Young Sound, Rysgaard et al., 1999; NCP = +0.001 $gO_2\,m^{-3}d^{-1}$ 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 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, it is not clear whether the photosynthetic activity in the surface waters ~~may~~had not ~~have~~ commenced during the study period, or ~~it may have been~~was 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 ± 0.013 $gO_2\,m^{-3}\,d^{-1}$. 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 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.~~processes not occurring in the incubations (such as sea algal photosynthesis on the underside of the sea ice). 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.

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 S_0) can be estimated using $S/S_0 = (1 - \alpha)\exp(-k_s z_s - k_i z_i)$, where α 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 m^{-1} and 0.9 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 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. 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. (see Table 1). 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 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 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.

Competing interests

The authors declare no competing interests.

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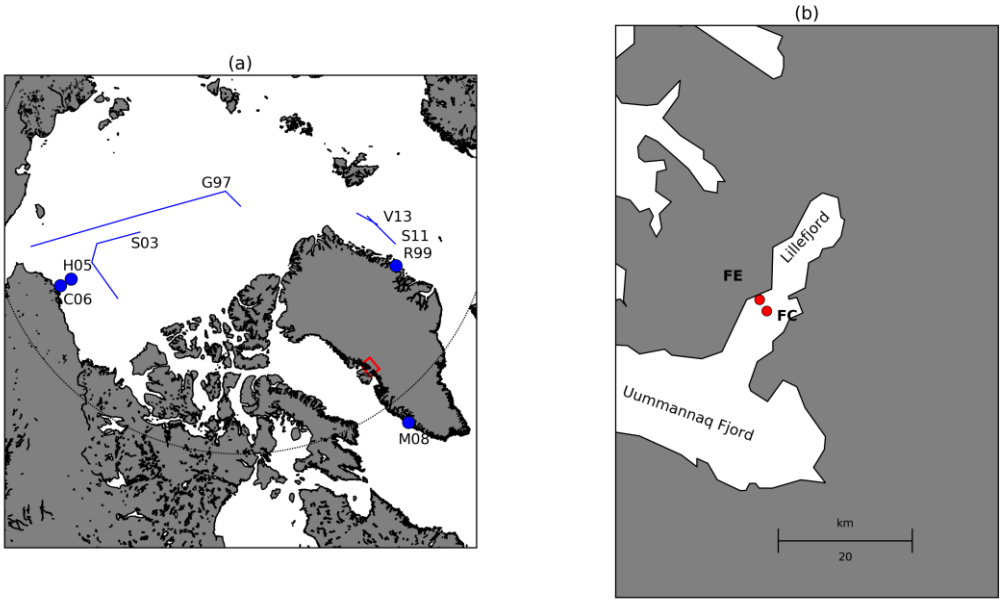


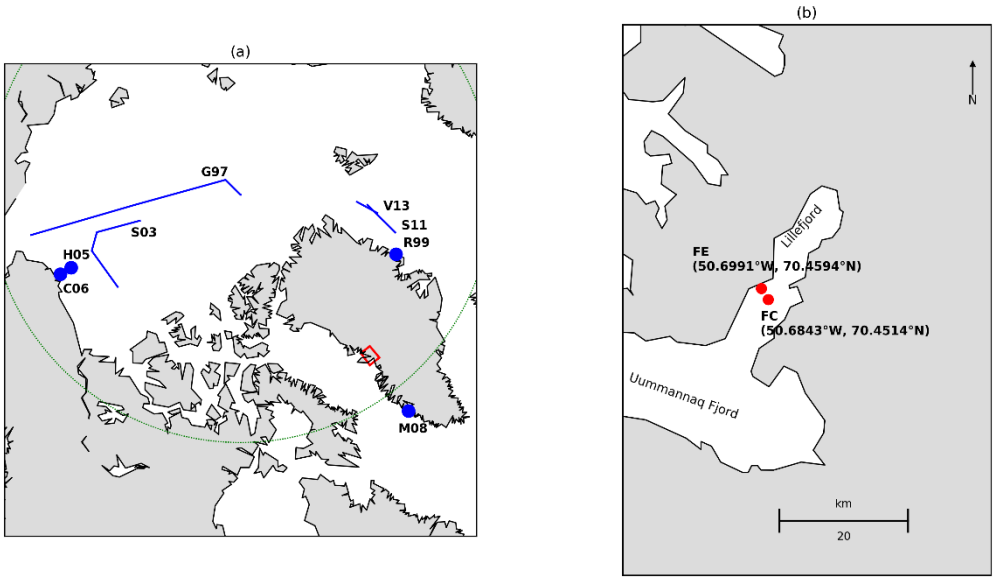
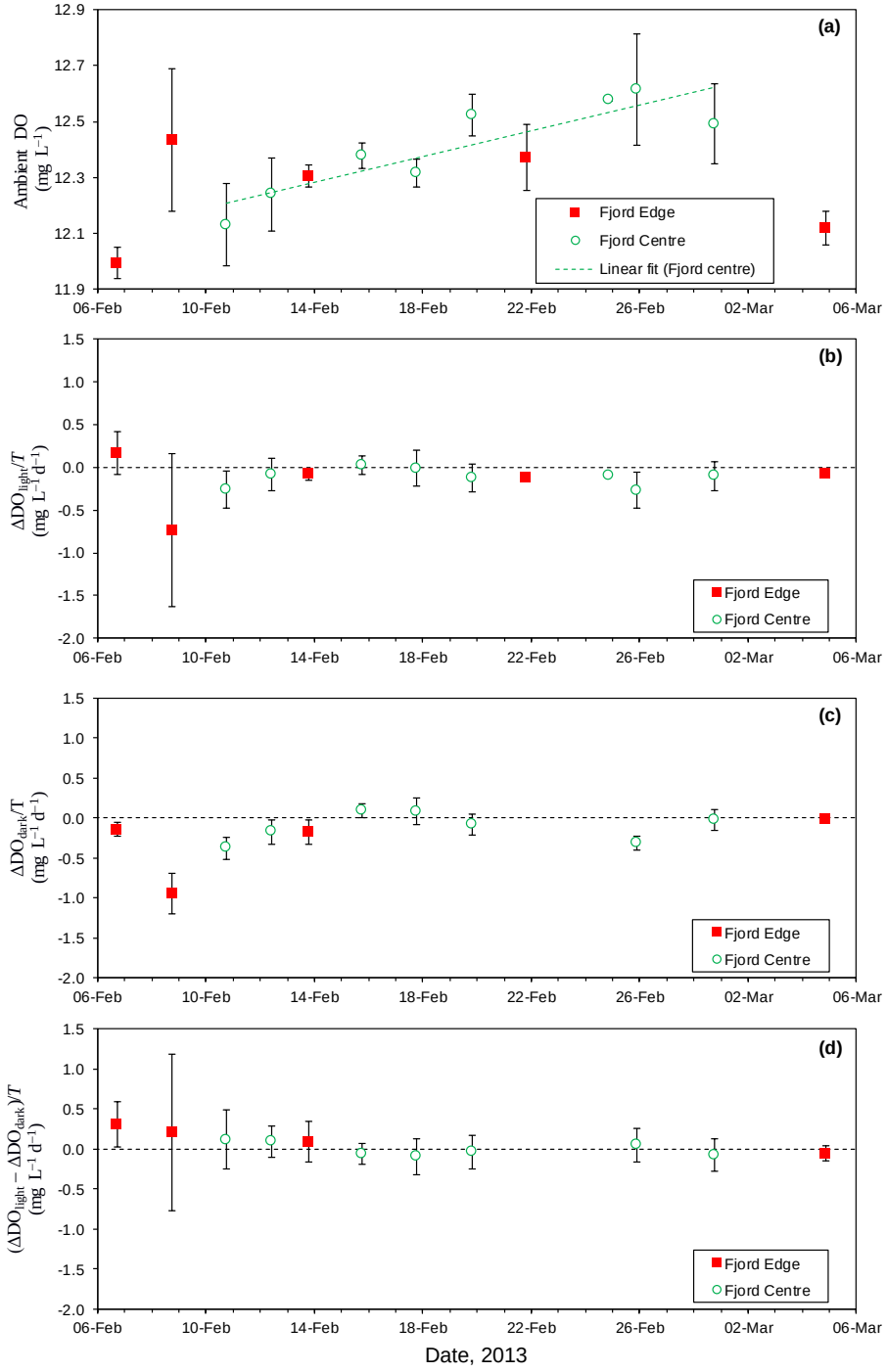


Figure 1: (a) Locations where microbial metabolism has been measured in the water column under sea ice (minimum sea ice cover 80%). Abbreviations follow Table 1. Positions of points and transects are approximate, and are based on maps in the corresponding publications. The Arctic circle is marked in green and the red box shows the location of Lillefjord, west Greenland. (b) Location of the fjord edge (FE) and fjord centre (FC) study sites. Coastline data are from https://www.soest.hawaii.edu/pwessel/gshhg/.



405

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 (ΔDO_{light} / T), interpreted as the net community production rate (NCP); (c) rate of change of DO in the dark incubation bottles (ΔDO_{dark} / T), interpreted as the respiration rate (CR); (d) the difference ($\Delta DO_{light} - \Delta DO_{dark}$) / T, interpreted as the photosynthesis rate (GPP). Times are local time in Greenland (UTC-3) in 2013.

410

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 ^{14}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^{-2} d^{-1} 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_2 m^{-3} d^{-1}	GPP gO_2 m^{-3} d^{-1}	CR gO_2 m^{-3} d^{-1}	SOURCE
Arctic Ocean 75-90N Chukchi Sea to North Pole	0-60[a]	>80 %	Inc (^{14}C), 12 hr, artificial light.	July-Aug 1994	NR	0.0004 to 0.0025 [b]	NR	G97
Young Sound, E Greenland 74N ~800 m from coast, in fjord Ice thickness decreasing from ~2m	0-35	100 %	Inc (^{14}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
			Inc (DO), dark, 72 hr	Autumn-winter 1997	NM	NM	0.019 ± 0.014	
				Midwinter 1997-8	NM	NM	0.008 ± 0.008	
				Spring-summer 1998	NM	NM	0.027 ± 0.019	
Chukchi Sea	0-~90	>80 %	Inc (^{14}C) artificial light	Spring 2002	<0.003	NM	NM	H05
Chukchi Sea		100 %	Inc (DO & ^{14}C)	May-June 2004				C06[b]
	Surface				+0.07 ± 0.12	NM	0.17 ± 0.32	
	15% light				+0.22 ± 0.11	NM	0.06 ± 0.01	
	1% light				+0.08 ± 0.13	NM	0.08 ± 0.01	
Kangerluarsunnguaq, W Greenland, 64N. Fjord ~100m deep.	0-50		Inc (^{14}C), 2 hr, artificial light, 4°C.					M08
Ice increasing 0-50 cm thickness		100 %		Dec Mar 2006-7	<0.001	NM	NM	
Ice ~60 cm thickness		100 %		Apr 2007	+0.001	NM	NM	
Fram Strait, 75-78N	0-20	>80 %	Inc (DO), 24 hr, in-situ.	Apr-May 2008				S11
Site C1, 78N					+0.056	bd	bd	
Site E, 75N					–0.006	+0.029	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				Feb-Mar 2013				
Fjord edge	Surface	100 %	Inc (DO) in-situ, 1-4 days.		–0.17 ± 0.19	+0.19 ± 0.30	0.36 ± 0.24	This study
			Ambient DO		–0.001 ± 0.031			
Fjord centre	Surface	100 %	Inc (DO) in-situ, 1-4 days.		–0.10 ± 0.07	–0.01 ± 0.10	0.09 ± 0.07	
			Ambient DO		+0.023 ± 0.013			

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 changes in dissolved oxygen in the light bottles and in the dark bottles ($\Delta DO_{light} - \Delta DO_{dark}$).

Start time (2013)	Hole	T d	O_2 start $gO_2\ m^{-3}$	N_L	ΔO_2 Light $gO_2\ m^{-3}\ d^{-1}$	N_D	ΔO_2 Dark $gO_2\ m^{-3}\ d^{-1}$	$L - D$ $gO_2\ m^{-3}\ d^{-1}$	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†	2	–0.12± 0.05†	---	---	---	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.
Overall	**FE**		**12.24 ± 0.08**	**18**	**–0.17 ± 0.19**	**14**	**–0.36 ± 0.24**	**0.19 ± 0.30**	
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†	2	–0.10± 0.03†	---	---	---	30-30 mm snow. Clear sky.
25 Feb 21:29	FC	1.8	12.61 ± 0.20	2	–0.27± 0.03†	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 2nd.
Overall	**FC**		**12.38 ± 0.05**	**34**	**–0.10 ± 0.07**	**32**	**–0.09 ± 0.07**	**–0.01 ± 0.10**	

Response to reviewers' comments

Reviewer 1: As the authors have measured temperature and salinity for each of the experiments (if not samples), I wonder, why this data (though not being crucial) is not included in the data set. I also wondered, why the data file archived at PANGAEA did not include the full data set, i.e., DO results for each of the individual samples. Instead, it only included the results listed in Table 2 of the manuscript, i.e. mean values and uncertainties/ranges for the different experiments carried out in the fjord center and at its edge. I would like to ask the authors to comment on this.

Response: There was little variation in ambient temperature and salinity (-1.5 to -1.7°C, and 32.6 to 32.8 psu). This is noted in Section 3, first paragraph. We originally only archived the summary of results as this was considered the most useful format; however, we will add results for individual bottles to the archive along with temperature and salinity measurements.

Reviewer 1: page 5, second paragraph: Could you please add an explanation why there aren't any "dark" samples for February 22? Furthermore, what was the reason for changing the incubation time (1 vs 2 vs 4 days), and was there any notable effect?

Response: We had some instrument/equipment failures while installing the bottles, so sometimes we were unable to use the full set of 10. We have explained this in the methods [approx. Line 55]. While annoying, this left us with spares with which to try longer incubation times, which was useful because we were finding that variability of the 1-day incubation results was high compared with the magnitudes of any changes. Longer experiments allowed potential for a stronger signal, but have the disadvantage that any methodological artefacts arising from the system being closed rather than open are also likely to increase during longer incubations. We do not have enough data to confidently assess whether or not the longer incubation times were helpful. An extra paragraph explaining the incubation times has been added to the methods.

Reviewer 1: page 5, line 183: Figure 2a presents "ambient DO", not temperature and salinity as mentioned in the text. It would be useful to have this data included in the data file as well as in Figure 2.

Response: The reference to Fig. 2a has been moved to the end of the paragraph (following the description of ambient DO). Ambient T and salinity data are now included in the archived data set.

Reviewer 1: page 6, line 191: please, add a reference to Figure 2c at the end of the sentence.

Response: This figure reference has been added.

Reviewer 1: page 6, line 204: This should be Figure 2c ("dark"), not 2b, which shows results for the light incubations.

Response: We have changed 2b to 2c.

Reviewer 1: page 7, line 261: please, add some references at the end of the sentence ". . . in the Arctic."

Response: We have added a reference to Table 1 which summarises some previous studies in the Arctic.

Reviewer 1: Table 1: Please, add the incubation time (or a respective range) for the results originating from the present study. They are provided for the other studies listed in the table.

Response: Incubation times have been added in Table 1.

Reviewer 1: Figure 1: The figure would clearly benefit from having some map coordinates. I can only guess that the black circle shown in Fig. 1a indicates the polar circle. What topography data set is used ?

Response: We have added co-ordinates in Fig. 1b and revised the caption of Fig 1a to include the polar circle. The map does not show topography, but the source of the land outline has now been noted in the caption.

Reviewer 2: I think this is a unique and essential dataset contributing immensely to the body of evidence on climate change issues. Extreme environmental conditions at the experiment sites were carefully mitigated to collect bias-free data. The only concern that I would have is that as a data paper, this manuscript should be free of any interpretation of the data. Such comments tend to suggest the author's opinions and views to the readers. The authors should avoid such an explanation leaving just a general assessment as to the ways the data can be used, e.g., as a validation or calibration data set of remotely sensed observations.

Response: Similar points were raised by Reviewer 2 and Reviewer 3. While the paper describes the data and results, with little interpretation because we do not have any supporting data with which to make any detailed interpretations, we have removed some interpretation from the Discussion section. Following these edits the Discussion section is now restricted to: (1) estimates of photosynthesis rates using differences between light and dark incubations, as this calculation is a standard part of the light/dark incubation method; (2) a brief comparison between the incubation results and ambient dissolved oxygen results, as these two approaches show some important differences that highlight the advantage of using the two methods simultaneously; and (3) a short note on the potential influence of changes in under-ice irradiance. Where relevant we have retained a limited comparison of our results with previous studies, as this puts our results in the context of this previous work, but we have not suggested any reasons for the similarities/differences.

Finally, to reflect the above edits, we have changed the last part of the Abstract to: "Averaged over the full study period, dark incubations showed statistically significant decreases in DO of –0.36 ± 0.24 (near shore) and -0.09 ± 0.07 $gO_2\ m^{-3}\ d^{-1}$ (fjord centre), indicating respiration rates that were 2-20 times greater than rates previously reported under sea ice in the Arctic. Meanwhile, a lack of significant evidence for photosynthesis suggests that the rate of photosynthesis – if it was occurring – was much lower than that of respiration. The data also show no significant evidence of a temporal trend in metabolism rates over the study period; however, ambient sea water DO increased significantly at the fjord centre (0.023 ± 0.013 $gO_2\ m^{-3}\ d^{-1}$), possibly attributable to processes not occurring in the incubations (such as sea ice algal photosynthesis). These data may improve our understanding of microbial activity in the fjord during winter, and its contribution to Arctic ecosystems under present and future conditions."

Reviewer 2: Below are some minor things I noticed while reading the manuscript.

L13 and through the text: '±.' I would not use this symbol in this context because it indicates a range. What you are trying to say is: 'one standard deviation.' And as you know, the SD is a positive root square of the variance. This note is just a cosmetic one. In some sciences, this is still acceptable.

Response: Presenting results as a mean ± SD or as a mean ± error is a widely used convention in this field, and for consistency (and clarity) we have followed this convention. We also note that there is a difference between mean ± SD and mean ± error; except where noted, we have used the latter format. Errors were calculated as described in Section 2.1.

Reviewer 2: L94. 'shortly after the transition from polar night to spring conditions.' How many days since the end of the polar night?

Response: We have added that the end of the polar night was on 21 January.

Reviewer 2: L151. '...the of the last…'

Response: this typo has been fixed.

Reviewer 2: L209 'variance' change to 'standard deviation.'

Response: This has been changed.

Reviewer 2: Add coordinates and the north arrow to the maps. Add the year to the caption of the graphs and tables.

Response: These have been added.

Reviewer 3: I would suggest changing a title. In my opinion 'marine productivity' should be exchanged with e.g. "marine microbial respiration", as the second term more clearly indicates what is actually provided and was directly measured contrary to 'productivity', which can only be indirectly retrieved from oxygen measurements and which in practice was not observed at all.

Response: We agree the title needs changing but instead have changed 'marine productivity' to 'marine microbial activity' as our experiments were designed to measure net microbial productivity rather than just respiration.

Reviewer 3: Abstract: I think the main finding "rate of photosynthesis – if it was occurring – must have been much smaller than that of respiration" should be mentioned in the Abstract.

Response: We have noted this in the abstract. This part of the abstract now reads: "Averaged over the full study period, dark incubations showed statistically significant decreases in DO of –0.36 ± 0.24 (near shore) and -0.09 ± 0.07 $gO_2\ m^{-3}\ d^{-1}$ (fjord centre), indicating respiration rates that were 2-20 times greater than rates previously reported under sea ice in the Arctic. Meanwhile, a lack of significant evidence for photosynthesis suggests that the rate of photosynthesis – if it was occurring – was much lower than that of respiration."

Reviewer 3: Introduction: generally, it is well written, informative and well explaining the importance of the study. I think it could also refer to the work by Assmy et al. 2017 (Scientific Reports): Leads in Arctic pack ice enable early phytoplankton blooms below snowcovered sea ice.

Response: We have incorporated this study into the introduction.

Reviewer 3: Please provide a reference to the statement "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"

Response: Brown and Arrigo (2012) used remote sensing to study the link between increasing NPP and reduced sea ice cover; this reference is included at the end of the above sentence.

Reviewer 3: Dataset: it is stated that up to 10 samples per experiment were analysed. Also in Pangea it is written that datasheet should contain 167 data points, however the database I had an access contain only 13 records, which I assume are already the means of the particular measurements. However, as the errors of the means are substantial, I do think it would be great to have a possibility to work on all the data (measurements).

Response: We will add results from individual bottles to the data archive on Pangea.

Reviewer 3: If the effect of the glacier was taken into consideration in the sampling design, ideally if data could be supplemented by e.g. turbidity levels. The same applies to providing the data that were measured for sure (temperature, ice thickness).

Response: There will have been very little runoff from the glacier in February/March, and the sampling design just compared near-shore, shallow water with much deeper water in the fjord centre. The effect of large meltwater inputs in the summer

would of course be a very interesting future study as the ice sheet has been found to be exporting nutrients to the surrounding coastal waters (e.g., Hawkings et al., 2014 and Lawson et al., 2014 which we have cited in the paper).

Reviewer 3: Results: I cannot find those results : "Throughout the study period, the sea water temperature and salinity varied between -1.5 and -1.7o C, and between 32.6 and 32.8 psu, respectively (Fig. 2a).", neither at the Figure nor in the dataset.

Response: The reference to Fig. 2a has been deleted as those results are not plotted. The temperature/salinity measurements are now in the archived data.

Reviewer 3: Why there is no 'rate of change' on Fig. 2c & 2d for the 21.02.2013 in the Fjord Edge station ?

Response: no dark bottles were used in that incubation. Therefore, there is no respiration value in Fig 2c and no corresponding photosynthesis value in Fig. 2d for that date.

Reviewer 3: According to the results description, which is as follows: "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)" there was no production occurring ! That's why I proposed to change the title.

Response: The title has been changed as noted above.

Reviewer 3: How is the result described in the Abstract "Averaged over the full study period, dark incubations showed statistically significant decreases in DO of –0.36 ± 0.24 (near shore) and -0.09 ± 0.07 gO_2 m^{-3} d^{-1} (fjord centre), indicating respiration rates that were 2-20 times greater than rates previously reported under sea ice in the Arctic." obtained? What kind of calculation stays behind ? Is that a difference between first and last sampling ?

Response: These values are calculated using the bottles from all incubations at the respective hole.

Reviewer 3: Conclusions: I am afraid some data interpretations may be too far reaching and cannot be supported by the dataset provided: e.g., "at Lillefjord, then it is likely that ice algal photosynthesis commenced earlier than photosynthesis in the underlying water column" "in this study, the difference is most likely attributable to net production by sea ice algae (which would increase DO in the ambient sea water), contrasting with net respiration in the underlying water 270 (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."

Response: Reviewer #2 also commented on the interpretations being too detailed. Therefore, we have reduced the level of interpretation as described in the corresponding response to Reviewer #2 above.