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Plankton community and bacterial metabolism in Arctic sea ice leads during summer 2010

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ABSTRACT

Microbial plankton metabolism was examined during summer 2010 in sea ice-influenced waters of the Fram Strait, eastern Arctic Ocean. Rates of gross primary production and community respiration were tightly coupled over a wide range of values (33 ± 3 – 143 ± 6 and 20 ± 3 – 126 ± 6 mmol O₂ m⁻² d⁻¹, respectively) leading to a prevalence of positive net community production. The high variability in community respiration, similar to that of gross primary production, suggests that heterotrophic metabolism may exhibit a significant response to environmental change. Bacterial respiration was assessed at similar time scales to bacterial production measurements, by determining the *in vivo* INT reduction capacity without pre-filtering the community. Bacteria seem to play a major role in total community respiration, contributing between 5% and 61% of total community respiration, indicating that a high fraction of the organic carbon in Arctic planktonic food webs could flow through these microbes.

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1. Introduction

Sea ice extent and thickness is a major factor influencing marine planktonic productivity in the Arctic. On the one hand ice cover increases light attenuation, reducing the solar irradiance available in the underlying water column with associated shallowing of the euphotic layer (Sakshaug, 2004) and limitation of primary production (Arrigo et al., 2008; Pabi et al., 2008; Wassmann et al., 2006). Phytoplankton may also be subject to nutrient-limitation in the euphotic zone due to melting ice inducing haline vertical stratification that may act as a natural barrier constraining nutrients beneath the mixing layer. On the other hand the same haline stratification may increase the residence time of phytoplankton in the euphotic zone promoting primary production (Carmack and Wassmann, 2006; Cota et al., 1996; Harrison and Cota, 1991). These interactions of light and nutrients, and their temporal and regional variability, are important but poorly understood factors controlling primary production in the Arctic (Popova et al., 2010, 2012).

Much of the current knowledge of the variability of primary production and ability to predict associated ecosystem behaviour in the Arctic depends on numerical models utilising ocean colour data from satellites (Arrigo et al., 2008; Hill et al., 2013; Pabi et al.,

2008; Popova et al., 2012; Slagstad et al., 2011). Despite their increasing use and generally reliable results, numerical models and associated satellite data have several limitations that could lead to errors in the estimation of primary production rates in the optically complex Arctic (Arrigo et al., 2011). Resolving these difficulties requires validating ocean colour results with field data and deriving robust relationships relating ocean colour to primary production. Such models are, however, validated using *in situ* measurements of primary production determined by the ¹⁴C incorporation approach which, when applied over a 24 h period, is considered to derive values between gross and net primary production (Marra, 2009).

The accurate assessment of marine ecosystem productivity and associated carbon flow requires not only measurements of primary production, but also knowledge of the balance between gross primary production (GPP) and community respiration (CR); *i.e.* net community production (NCP). NCP should, in theory, be a more comprehensive estimate of plankton community metabolism with which to validate ocean colour data than primary production derived from ¹⁴C incorporation; however Arctic CR and NCP data sets are scarce compared to those for primary production obtained using the ¹⁴C approach (Cottrell et al., 2006; Kirchman et al., 2009; Nguyen and Maranger, 2011; Nguyen et al., 2012; Regaudie-de-Gioux and Duarte, 2010; Sherr and Sherr, 2003; Vaquer-Sunyer et al., 2013). Further, there is no model currently available to calculate CR from satellite data and therefore predict the consequences of environmental change. Moreover, CR will respond to community structure and the availability of

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allochthonous organic matter, in addition to physical forcing of and variability in primary production, thus complicating model-prediction of heterotrophic community metabolism.

The few reports on plankton metabolism available from Arctic regions show that metabolic balance is highly dependent on the growth phase of the community (Vaquer-Sunyer et al., 2013). They also demonstrate that metabolic balance can be difficult to determine due to inconsistencies between seasons in the reported relationships between *in situ* measurements of Arctic primary production and community respiration (Cottrell et al., 2006; Regaudie-de-Gioux and Duarte, 2010; Vaquer-Sunyer et al., 2013). In the western Arctic, and in accordance with observations in temperate and tropical oceans (e.g. Aristegui and Harrison, 2002 and Duarte and Agusti, 1998), Cottrell et al. (2006) reported CR to be less variable than primary production, which in turn influences NCP and associated export potential. In the eastern Arctic, Regaudie-de-Gioux and Duarte (2010) found that a significant fraction (47%) of the planktonic communities they observed in the Fram Strait–Svalbard region were net heterotrophic. In this latter study the threshold GPP for metabolic balance (i.e., $GPP=CR$, calculated from the relationship between GPP and NCP) was found to be much higher than in the Southern Ocean. The results were also interpreted as indicating a prevalence of heterotrophic metabolism attributable to high allochthonous organic nutrient inputs into the Arctic Ocean. By contrast, Vaquer-Sunyer et al. (2013) collected data from the eastern Arctic, including in the Fram Strait–Svalbard region, during different seasons and years and reported net autotrophy for all seasons except winter.

Bacteria play an important role in plankton metabolism as they are responsible for a considerable component of CR and crucial for the remineralisation of organic material (Kirchman et al., 2009; Nguyen and Maranger, 2011; Nguyen et al., 2012; Nielsen and Richardson, 1989; Pomeroy and Wiebe, 2001). The dynamics of these microbes have a major impact on the efficiency of carbon transfer from the phytoplankton to higher trophic levels, and therefore the amount of carbon available to be vertically transported to the deep ocean (Jiao et al., 2010). Bacterial respiration (BR) is poorly characterised in sea ice-influenced Arctic waters and most estimates have been made using empirically-derived conversions from CR measurements (Nguyen and Maranger, 2011) or by measuring changes in dissolved oxygen concentration after long (~24 h) incubations of communities which have been size-fractionated (and hence disrupted) by pre-filtration (Cuevas et al., 2011; Kirchman et al., 2009). These incubation times are significantly longer than the timescales of bacterial production (BP) measurements (typically 1–4 h). Respiration measurements derived from such disrupted communities may therefore be inaccurate due to modification of organic matter availability, competition and predation (Aranguren-Gassis et al., 2012). There is therefore a clear need for more information on phytoplankton and bacterial respiration in the Arctic, and the relationship between respiration rates and factors that will be altered by changing ice cover (Nguyen and Maranger, 2011; Wassmann, 2011).

The aim of the present study was to estimate the planktonic metabolic balance, and test the relationships existing between GPP and CR, in sea ice-influenced waters of the Fram Strait in the eastern Arctic. For the first time, CR and BR were estimated in the Arctic from *in vivo* reduction capacity of 2-(ρ -iodophenyl)-3-(ρ -nitrophenyl)-5phenyl tetrazolium salt (INT) (*in vivo* INT) after short (2–5 h) incubations of unfractionated plankton communities. *In vivo* INT can be used as a proxy for respiration rates (García-Martín et al., in prep), although it has several limitations (Maldonado et al., 2012). The methodological approach also reduces the problems associated with differential incubation times used in previous comparisons of Arctic BP and BR measurements. The resulting data contributes to the limited information available on Arctic GPP, CR, NCP and BR, thereby improving significantly our understanding of microbial processes in this rapidly changing region.

2. Materials and methods

2.1. Study site

The study was undertaken between 23 June and 9 July 2010 as part of the UK ICECHASER II research cruise on the RSS James Clark Ross (cruise JR219). Eight ice lead stations were sampled in the Fram Strait (Fig. 1, Table 1). Six stations (I2, I3, I5, I6, I8, I9, referred to hereafter as northern Fram Strait stations) were located in the northern Fram Strait and were sampled as the ship, anchored to a large (1.7 km²) ice floe, drifted for 9 days to the south-west. The remaining two stations (GS1 and GS2, referred to hereafter as eastern Greenland Shelf stations) were located in the south-western Fram Strait, overlying and adjacent to the east Greenland shelf. These two locations are influenced by different water masses: the northern Fram Strait stations by the relatively warm

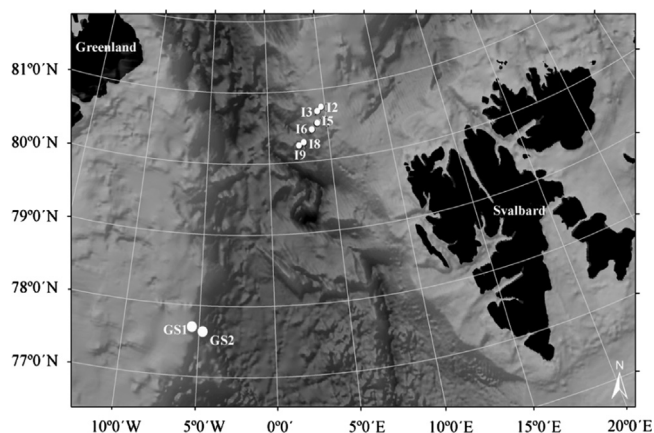


Fig. 1. Map of the stations sampled in the Fram Strait.

Table 1

Dates, acronym, location, CTD rosette number and physicochemical descriptors of the stations sampled in the Fram Strait (PSW=Polar surface water).

Sampling date	Station name	Station acronym	Latitude	Longitude	CTD No	Descriptors
23/06/2010	Ice2	I2	80.74 N	4.65 E	14	9/10 Ice cover, stratified, low nutrient, shallow PSW
24/06/2010	Ice3	I3	80.69 N	4.32 E	17	9/10 Ice cover, stratified, low nutrient, shallow PSW
26/06/2010	Ice5	I5	80.52 N	4.17 E	20/21	9/10 Ice cover, stratified, low nutrient, shallow PSW
27/06/2010	Ice6	I6	80.44 N	3.66 E	23	9/10 Ice cover, high nutrients, deep PSW
29/06/2010	Ice8	I8	80.27 N	2.92 E	28	9/10 Ice cover, stratified, low nutrient, shallow PSW, high chlorophyll
30/06/2010	Ice9	I9	80.23 N	2.5 E	30	8/10 Ice cover, stratified, low nutrient, shallow PSW, high chlorophyll
08/07/2010	Greenland Shelf1	GS1	77.78 N	5.6 W	49	6–8/10 Ice cover, stratified, low nutrient, high chlorophyll
09/07/2010	Greenland Shelf2	GS2	77.60 N	5.19 W	52 / 53	5–6/10 Ice cover, stratified, low nutrient waters, shallow PSW

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