# Seasonal patterns in Arctic planktonic metabolism (Fram Strait - Svalbard region)

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## Abstract

The metabolism of the Arctic Ocean is marked by extreme pronounced seasonality and spatial heterogeneity associated with light conditions, ice cover, water masses and nutrient availability. Here we report the marine planktonic metabolic rates (net community production, gross primary production and community respiration) along three different seasons of the year for a total of eight cruises along the western sector of the European Arctic (Fram Strait – Svalbard region) in the Arctic Ocean margin: one at the end of 2006 (fall/winter), two in 2007 (early spring and summer), two in 2008 (early spring and summer), one in 2009 (late spring – early summer) and two in the springs of 2010 and 2011 . The results show that the metabolism of the western sector of the European Arctic varies throughout the year, depending mostly on the stage of bloom, which is mainly determined by availability of light and nutrients. Here we report metabolic rates for the different periods, including the spring bloom, summer and the dark period, increasing considerably the

empirical basis of metabolic rates in the Artic Ocean, and especially in the European Arctic corridor. We also report a rough annual metabolic balance for this area of the Arctic Ocean, resulting in a net community production of 108 g C $m^{-2}$ $year^{-1}$.

## 1. INTRODUCTION

The climate of the Arctic marine environment is characterized by extreme seasonality in solar radiation, ice cover and atmospheric temperature and, to a lesser extent, water temperature (Carmack et al. 2006; Carmack and Wassmann 2006). This variability should be reflected in significant variability in pelagic metabolism of the Arctic Ocean, with negligible photosynthetic primary production during the extended dark period and respiration rates affected by the ensuing variability in the supply of organic matter and changes in water temperature from winter to summer. Hence, community respiration must prevail over primary production in the dark, while primary production can be quite high during the light period (Hodal and Kristiansen 2008), when plankton communities receive photosynthetically-active radiation (PAR) 24 hours per day (Sakshaug and Slagstad 1991; Sakshaug et al. 1994). However, respiration rates are also expected to increase in the summer due to increased temperatures and increased supply of dissolved organic matter. Hence, both gross primary production and respiration rates are expected to show high seasonal variability in the Arctic Ocean.

Community metabolism in Arctic planktonic communities is expected to be very variable as it involves extreme transitions from complete darkness to continuous daylight. Additionally, increased advection of Atlantic waters into the Arctic generates high spatial variability and fronts (Dmitrenko et al. 2008; Ivanov et al. 2009), which may mask the seasonal signal of planktonic metabolism.

Although estimates of Arctic primary production are available (e.g. Rao and Platt 1984; Sakshaug 1997; Sakshaug 2004; Wassmann et al. 2006a; Pabi et al. 2008), reports of direct measurements of planktonic metabolism in the Arctic are sparse, much more so than those for Antarctic waters (e.g. Agusti et al. 2004; Agusti and Duarte 2005; Dickson and Orchardo 2001; Lefèvre et al. 2008; Robinson et al., 1999), and are limited to few publications, as one report of summer metabolism in the coastal waters of the Chukchi Sea sector (Cottrell et al. 2006), two reports from the Canadian Basin, reporting only respiration rates, just one of the

components involved in the assessment of metabolic balance (Apollonio 1980; Sherr and Sherr 2003), four reports of summer primary production assessed using $^{14}C$, two in the Chukchi Sea (Hameedi 1978; Cota et al. 1996), one in the Baffin Bay (Harrison et al. 1982), one in the Central Arctic (Olli et al. 2007), and one reporting summer metabolism (gross primary production, community respiration and net community production) in 2007 in the region studied here (Regaudie-de-Gioux and Duarte 2010). This last study is included here to provide a more complete assessment of the metabolism in this area, as it was conducted in the same area using the same methods. There are a considerable number of studies reporting integrated values for planktonic metabolism (e.g. English 1961; Sokolova and Solovyeva 1971; Alexander 1974; Subba Rao and Platt 1984; Hodal and Kristiansen, 2008; Ardyna et al., 2011). However, as integration depths vary between studies, these studies are not included here. Whereas the previous observational data were insufficient, the set of estimates reported here provides the first empirical basis with which to establish patterns in the seasonal variability in planktonic metabolism in the European Arctic Ocean. Additionally it allows us to provide a first approximation at the annual balance between gross primary production and plankton respiration in these communities. Although the estimates are rough, the seasonal coverage at the regional scale provided here compares favourably with the state of knowledge available for any other ocean region in the world (Robinson and Williams 2005).

The characterisation of the seasonal patterns of variability in plankton community metabolism in the Arctic Ocean is not only important to gain additional understanding on the functioning of these communities and their role in the regional carbon budget, but it is also essential to provide baseline data to detect changes in Arctic planktonic metabolism with climate change. The Arctic Ocean is warming at rates three times faster than the average rate of warming of the global ocean (ACIA 2004; Trenberth et al. 2007) and is projected to continue to do so in the future (Houghton 2005; Walsh 2008). Indeed, impacts are already evident as the summer ice cover experienced a sudden decline resulting in a historical minimum in the summer of 2007, with a 43% reduction in the minimum ice extent relative to the ice extent in 1979, a loss equivalent to more than twice the area of Alaska (Kerr 2007), and a reduction of more than the 40% of multiyear ice volume from 2005 to 2008 (Kwok et al. 2009). Recently, a new historical minimum has reached in September 2012, with a decrease of a 760000 $Km^2$ below the previous record minimum extent in 2007 (http://nsidc.org/arcticseaicenews/). Reduced ice cover increases underwater irradiance to support primary production and may also, because of the enhanced supply of photosynthetic

organic matter, lead to increased plankton community respiration in Arctic waters. Warming is also expected to directly affect metabolic rates, as temperature plays an important role in regulating metabolic processes (Iriberri et al., 1985; White et al., 1991), and metabolic rates are expected to increase exponentially with water temperature (Brown et al., 2004).

Here we evaluate seasonal and spatial variability in planktonic gross primary production (GPP), net community production (NCP) and community respiration (CR) in the Fram Strait and Spitsbergen waters of the European Sector of the Arctic Ocean. Here we address the questions of whether the Western European Arctic sector is net autotrophic at the annual scale and whether the excess production during the light period suffices to meet the respiratory requirements during the Arctic dark period. We do so on the basis of eight cruises conducted in three contrasting periods of the year, late fall-early winter 2006, spring 2007, 2008, 2010 and 2011, the summers of 2007 and 2008 and late spring-early summer 2009 (Fig. 1).

## 2. Materials and Methods

### 2.1 Research area

The Fram Strait, located between Greenland and Svalbard, connects the North Atlantic and the Arctic Ocean with an important heat and mass exchange, with large quantities of heat transported polarward by the extended North Atlantic Current; the West Spitsbergen Current (WSC), which influences the climate in the Arctic region as a whole (Fig. 1, Hop et al. 2006). Ice outflow from the Arctic occurs at the western part of the Fram Strait along the East Greenland Current (EGC, Schlichtholz and Houssais 2002). The circulation is characterized by a generally southward EGC system on the western side along the Greenland slope and Shelf, and a generally northward WSC system in the eastern side. The WSC and EGC exchange water though counter-clockwise recirculation (Schlichtholz and Houssais 2002). The northward transport of warm Atlantic Water (AW) melts southward-drifting ice and maintains open waters north of Svalbard (Rudels et al. 2000). This area is hydrographically complex, including sharp gradients in plankton communities. During the cruise conducted in summer 2007 a pronounced intrusion of Atlantic waters was found north of Spitsbergen, with 71% of the stations in this area containing AW.

The Kongsfjorden-Krossfjorden fjord system is situated on the west coast of Spitsbergen (Svalbard), or at the eastern extreme of the Fram Strait (Fig. 1). This fjord system is mainly

125 affected by the poleward transport of water in the WSC and the mixing processes on the shelf
126 result in Transformed Atlantic Water in the fjord (Hop et al. 2006). The West Spitsbergen
127 Current plays a predominant role on the west coast of Svalbard, and directly influences open
128 fjords. Advection of warm water masses during late autumn and winter, together with
129 prevailing wind patterns and air temperatures, may prevent ice formation in the fjords (Hop et
130 al. 2006, Cottier et al. 2007). During December 2006, at the time of one of our cruises, the
131 Kongsfjorden was almost completely ice-free.

132 The Barents Sea is an advective shelf system where colder and less saline Arctic and
133 modified Atlantic waters encounter and interact with warm and saltier Atlantic water,
134 creating a mosaic pattern of water masses influencing biological production (Reigstad et al.
135 2002).

136 **2.2 Methods**

137 The cruises were conducted along the western European gateway of the Arctic Ocean,
138 including the Fram Strait, the large Kongsfjorden-Krossfjorden fjord system in Svalbard, the
139 western Barents Sea, the East Greenland Shelf, the Greenland Sea and North Spitsbergen
140 waters (Fig. 1).

141 Samples were collected in eight different cruises across five different periods of the year: the
142 dark period in the late fall- early winter, early spring, spring, late spring-early summer, and
143 summer (Table 1). Cruises were conducted in December, in April, in April-May, in May, in
144 May – June, in June, in July and in July- August, respectively. Seven stations were sampled
145 in December 2006 on board R/V *Jan Mayen* (Fig. 1, Table 1). Our two early-spring cruises
146 (2007 and 2008) were conducted in a pre-bloom situation, in heavily ice-covered waters on
147 board the icebreaker KV *Svalbard*. Twenty-two stations were sampled in July 2007 on board
148 R/V *Hespérides*; seven in summer 2008, eight in June 2009, seven in spring 2010 and twelve
149 in spring 2011, all on board R/V *Jan Mayen* (Fig. 1, Table 1).

150 Water samples were collected at different depths within the photic layer using a Rosette
151 sampler system fitted with a CTD for a total of 69 stations, during the cruise conducted in
152 April 2007 a 30 L GO-FLO or Niskin was used for 1 m samples. Samples were incubated for
153 48 hours in December 2006 and in April 2007, when metabolic rates were particularly low,
154 and for 24 hours in the rest of cruises. Planktonic metabolism was evaluated from the changes
155 in oxygen concentration in replicated (6 to 11 replicates, depending on season) narrow-mouth
156 Winkler bottles. A set of bottles was fixed immediately to evaluate the initial oxygen content.

157 The other sets of bottles were incubated in the light and the dark in water baths on deck at in
158 situ temperature, using neutral screens to reduce incident irradiance and to mimic the light
159 environment in situ during the summer and spring cruises. In December 2006 the Winkler
160 bottles were incubated for 48 h in the dark in a controlled temperature room inside R/V Jan
161 Mayen, as there were 24 hr of darkness at the time of sampling. As incubation conditions
162 mimic environment conditions the results are comparable with incubations performed in situ.
163 In early spring (April 2007 and 2008) incubations were conducted in situ, deploying a buoy
164 from the deck of the ship and mooring it to the ice edge. Winkler bottles were attached to
165 methacrylate supports and suspended at the same depth from which the samples had been
166 sampled, thereby being exposed to the same light and temperature conditions. The work
167 conditions were particularly challenging during the spring cruises, when low air temperatures
168 (mean ± SE = -13.1 ± 0.3ºC) lead to frequent and rapid freezing and breakage of Winkler
169 bottles during exposure and retrieval.

170 Community metabolism (gross primary production, community respiration and net
171 community production) was evaluated at 3 or 4 different depths per station, depending on the
172 cruise. During early-spring cruises the depths selected were 1 m, 5 m, 10 m and 20 m. During
173 the summer cruise in 2007, late spring- early summer cruise in 2009, and spring cruise in
174 2010 and 2011 the depths sampled were 1m, the depth of the chlorophyll maximum layers
175 (CML) and an intermediate depth between these two depths. In Spring 2010 a fourth depth
176 was sampled in three of the seven total stations, sampling two intermediate depths between
177 the surface and CML. In summer 2008 the selected depths were 1 m, 10 m, 20 m and the
178 CML; when CML was at or near 20 m incubations were also conducted at 5 m. During late
179 fall-early winter cruise only the surface (1 m) layer was assessed, as the temperature and
180 irradiance (complete darkness) profile were uniform across the upper water column.

181 Dissolved oxygen concentration was measured using high-precision Winkler titration,
182 following the recommendations of Carritt and Carpenter (1966), using a precise automated
183 titration system with potentiometric (redox electrode) end-point detection (Mettler Toledo,
184 DL28 titrator) (Oudot et al. 1988).

185 The experimental standard errors (SE) of $O_2$ determinations among replicate bottles varied
186 between 0.04 and 6.27 mmol $O_2$ $m^{-3}$, with a mean of 0.66 ± 0.03 mmol $O_2$ $m^{-3}$. These errors
187 represent a mean of 0.19% of the total value of the measurement, with the replicates of light
188 bottles supporting a higher error than initial and dark bottle replicates. Although the lower

189 range of these errors is close to the limit of analytical detection, reported to vary between 0.06
190 and 0.1 mmol $O_2$ $m_3$ (Robinson and Williams, 2005), the upper range of these errors is
191 considerably higher.

192 Community Respiration rates (CR) were calculated from the difference between the initial
193 oxygen concentration and the oxygen concentration in the dark bottles after incubation. Net
194 Community Production (NCP) was calculated from the difference between the oxygen
195 concentration in the clear bottles after incubation and the initial oxygen concentration. Gross
196 primary production (GPP) was calculated as the sum of NCP and CR rates. All the rates are
197 reported in mmol $O_2$ $m^{-3}$ $d^{-1}$ and standard errors were calculated using error propagation. This
198 method assumes equal respiration rates in the light and in the dark. This assumption may lead
199 to underestimation of CR and GPP, because respiration rates are likely to be higher during
200 daylight than during night (Grande et al. 1989; Pace and Prairie 2005; Pringault et al. 2007),
201 but does not affect NCP estimates (Cole et al. 2000).

202 Metabolic rates were integrated down to 20m. The selection of an integration depth in the
203 high Arctic is rather cumbersome. The two criteria most widely used in the literature, mixed
204 layer and a light reference (e.g. 1 % PAR) are difficult to apply. Regarding the photic layer,
205 the integration depth during the winter period should be 0, as it is dark around the day and 0
206 light penetrates to any depth; this rules out the light penetration as a criteria. The mixed layer
207 is also cumbersome, as ice melting in spring and summer leads to very shallow pycnoclines
208 and, correspondingly, the mixed layer in only of 2-3 m depth, much shallower than the photic
209 depth, and the water column can be mixed to considerable depths (> 100 m) in the winter due
210 to convective mixing. We chose to integrate down to 20 m across all cruises because this
211 depth is close to both the chlorophyll a maximum layer (23.5m) and to the mixed layer depth
212 (17m) located below the shallow thermocline in the summer. We assessed the sensitivity of
213 our estimates this choice of integration depth by also calculating metabolic rates integrated
214 down to 30 m depth. This exercise showed integrated metabolic rates to be rather insensitive
215 to the choice of either 20 m or 30 m as integration depth (cf. table S2).

216 Chlorophyll *a* was measured using a Turner Design AV-10 fluorometer, calibrated with pure
217 chlorophyll *a* (Sigma 6041). Triplicate samples (100-500 mL) were filtered onto Whatman
218 GF/F filters.

219 Samples for dissolved organic carbon (DOC) were taken during the cruises conducted in
220 summer 2007 and 2008. Dissolved organic carbon (DOC) measurements were performed on

10 ml water samples sealed in precombusted glass ampoules (450 ºC for 5 h) and kept acidified (pH 1–2) until analysis by high temperature catalytic oxidation on a Shimadzu TOC- 5000A. Standards of 44–45 and 2 μmol C $L^{-1}$, provided by D.A. Hansell and Wenhao Chen (Univ. of Miami), were used to assess the accuracy of the estimates.

Samples for total bacterial abundance (BA) were taken during the cruises conducted in summer 2007 and early-spring 2008, as well as in one station in the cruise conducted in the dark period in 2006. Total bacterial abundance (BA) samples were determined by flow cytometry by FACSCalibur Flow Cytometer (Beckton Dickinson) as described in Ortega-Retuerta et al. (2008).

Water masses were classified following descriptions from (Rudels et al. 2000), based on (Friedrich et al. 1995; Rudels et al. 1999). Polar Surface waters (PSW) were defined as surface waters with a salinity lower than 34.4 and temperature below 0 ºC, when these PSW are warmed and the temperature increases to higher temperatures than 0 ºC these waters are called warmed Polar surface waters (PSWw); waters with a salinity higher than 34.4 and potential temperature above 2 ºC are classified as Atlantic waters (AW) (Rudels et al. 2000). The mixed layer depth (MLD) was calculated from the vertical profile of density following the criteria outlined by de Boyer Montegut et al. (2004). The mixed layer depth (MLD) was not always defined.

Quantile regression was used to describe the temperature-dependence of the volumetric and integrated metabolic rates. The relationship between metabolic rates and temperature was described by fitting the relationship between the 90%, 50% (median) and 10% quantiles of the distribution of metabolic rates and water temperature. Quantile regression estimates multiple rates of change (slopes), from the minimum to maximum response, providing a more thorough description of the relationships between variables, which are missed by other regression methods focused on prediction of the mean value (Cade and Noon, 2003). Quantile regression can be considered as an extension of classical least squares estimation of conditional mean models to the estimation of a compilation of models for several conditional quantile functions, considering the median as the central parameter (Koenker, 2005).

An estimate of the GPP threshold for metabolic balance was assessed using the relationship between the GPP to CR ratio (GPP/CR) and the GPP. As this relationship includes GPP in both its dependent and independent variables, the null hypothesis of this relationship is not that the slope equals zero, but that it equals one. A different approach to calculate the GPP

253 threshold for metabolic balance free of this potential problem, was also used, based on
254 inferring the GPP at NCP = 0 from the fitted relationship between NCP and GPP. A third
255 possible approach to assess the GPP threshold for metabolic balance is using a logistic
256 regression between the Log CR and Log GPP. To calculate the GPP threshold for metabolic
257 balance the metabolic rates that were non- significant (i.e. < 2*SE) were not included when
258 calculating the above-mentioned relationships.

259 A first estimate of the annual metabolic rates in the western European Arctic sector was
260 derived using the integrated metabolic rates presented here classified into five distinct
261 periods. The fall/winter data were used to characterise the period extending from the end of
262 the 24 h daylight period to the end of the dark period (112 days). Early-spring data were used
263 to characterise the period from the onset of the light period to the start of the 24 h daylight
264 period (70 days). The spring data measured in 2010 and some of the stations measured in
265 2011 were used as representative of a bloom stage (14 days). The late-spring data and some
266 stations measured in spring 2011 were used as data for a post-bloom stage during the 24 h
267 daylight (70 days). The summer data was used to characterise the summer period of 24 h
268 daylight in the post-bloom stage and the beginning period of the rise of sunlight hours, to
269 include the months of July, August and September (92 days). Metabolic rates were calculated
270 for the duration of each of these periods (as the product of the mean rates and the period
271 duration) and the rates derived from these periods extrapolated to encompass a full year.

272 An estimate of the DOC needed to sustain community respiration during the dark period was
273 derived using the mean volumetric community metabolism integrated during that period (112
274 days). Conversion from oxygen to carbon was made assuming a 1.25 molar stoichiometry
275 between $O_2$ and C (Williams et al. 1979).

276 ## 3. Results

277 ### 3.1 Hydrological data

278 The air temperature ranged from – 25.2ºC in April 2007 to +7.95 in July 2007 and the
279 seawater temperature varied from minimum values of -1.85 ºC, recorded in spring 2007 on
280 the East Greenland Shelf, to maximum values of 7 ºC, recorded in summer 2007 in Atlantic
281 waters (Table 1). The average seawater temperature was lowest for the two early-spring
282 cruises (mean ± SE = -1.78 ± 0.01 ºC in 2007 and in 2008) which took place in the Arctic
283 Ocean outflow, followed by the other 3 spring cruises, and exceeded 2.4 ºC for the other
284 cruises (Table 1 and Fig. 2). These significant (ANOVA, $F = 16.72$, $p < 0.0001$) differences

285 in water temperature between cruises can partly be attributed to seasonal differences but also
286 to variability in the water masses sampled. Indeed, during early-spring cruises only Polar
287 Surface Water (PSW) was sampled, whereas during the other five cruises Atlantic Water
288 (AW) and warmed Polar Surface Water (PSWw) were also sampled. Differences in water
289 temperature were also attributable to spatial differences, as there were significant differences
290 in the temperature ($F = 11.02$, $p < 0.001$) among the various areas sampled (Barents Sea,
291 North Spitsbergen, central Fram Strait, Svalbard Fjords, Greenland Sea, East Greenland Shelf
292 and West Spitsbergen).

293 The average salinity varied between 30.42 in spring 2007 and 35.14 in late fall-early winter
294 2006 at depths sampled to measure metabolism (all depths above 40 m) (Table 1). The
295 salinity differed significantly among cruises (ANOVA, $F = 13.02$, $p < 0.0001$). These
296 differences reflect both the effects of ice melting and the distribution of Atlantic, saltier,
297 versus Arctic water at the stations sampled in the different cruises. Surface salinities differed
298 significantly among sampled areas (ANOVA, $F = 10.48$, $p < 0.0001$), reflecting the presence
299 of Polar Surface Waters transported southwards along the EGC and the ice melting on the
300 Svalbard fjords during spring.

301 Chlorophyll *a* concentrations at the stations and depths where metabolic rates were
302 determined were lowest during late fall-early winter 2006 ($0.02 \pm 0.02$ µg Chl *a* $L^{-1}$),
303 somewhat higher in early spring ($0.03 \pm 0.00$ µg Chl *a* $L^{-1}$ in 2007 and $0.11 \pm 0.02$ µg Chl *a*
304 $L^{-1}$ in 2008), higher in summer ($2.43 \pm 0.24$ µg Chl *a* $L^{-1}$ in 2007 and $2.11 \pm 0.34$µg Chl *a* $L^{-1}$
305 in 2008), and highest in spring 2009 ($2.55 \pm 0.22$ µg Chl *a* $L^{-1}$, Table 1 and Fig. 2).
306 Unfortunately, chlorophyll *a* analyses were not conducted for the cruises conducted in spring
307 2010 and 2011. Chlorophyll *a* content increased significantly with seawater salinity ($R^2 =$
308 $0.20$, $p < 0.0001$, $N = 122$) and seawater temperature ($R^2 = 0.08$, $p < 0.002$, $N = 122$) in the
309 cruises and stations where data are available. Consequently, there were statistically
310 significant differences in chlorophyll *a* concentration between water masses ($F = 6.55$, $p <$
311 $0.003$), with Atlantic water (mean ± SE = $2.90 \pm 0.41$ µg Chl *a* $L^{-1}$) having significantly
312 higher chlorophyll *a* content than Polar Surface Waters (PSW, mean ± SE = $1.25 \pm 0.31$ µg
313 Chl *a* $L^{-1}$), but comparable to warmed Polar Surface Water (PSWw, mean ± SE = $1.88 \pm 0.21$
314 µg Chl *a* $L^{-1}$). This partly reflects the bloom stage sampled in the different regions.
315 Unfortunately we do not have data available for the spring cruise in 2010 where apparently a
316 spring bloom was sampled. Mixed layer depth varied greatly between 5 m in summer 2007

and 67.7 m in the dark period of 2006, with a mean value of 17.0 ± 1.9 m for all stations and 25.8 ± 6.8 m for the cruise averages.

Dissolved organic carbon (DOC) concentration varied between 65.11 and 132.65 µmol C $L^{-1}$. DOC concentration were comparable in Atlantic waters (mean ± SE = 93.24 ± 5.20 µmol C $L^{-1}$), than in warmed Polar waters (91.12 ± 3.55 µmol C $L^{-1}$), and were lower in Polar waters (78.71 ± 2.26 µmol C $L^{-1}$), although this difference was not significant ($p > 0.05$). The average DOC concentration (mean ± SE = 89.01 ± 2.46 µmol C $L^{-1}$) was comparable to that previously reported in the same area, 104 ± 25.7 (Kritzberg et al. 2010) and 93.95 ± 54.526 µmol C $L^{-1}$26 µmol C $L^{-1}$ (Tovar-Sánchez et al. 2010).

## 3.2 Metabolic rates

### *3.2 .1 Volumetric metabolic rates*

Net Community Production (NCP) ranged broadly from -21.7 ± 1.9 for strongly heterotrophic communities in summer 2007 to 81.6 ± 0.7 mmol $O_2$ $m^{-3}$ $d^{-1}$ for strongly autotrophic communities in spring 2011 (Tables 2 and S1, supporting material). NCP differed significantly between cruises, with higher NCP in spring 2010 and 2011 than for the other cruises (mean ± SE = 23.9 ± 3.1 mmol $O_2$ $m^{-3}$ $d^{-1}$ and 19.1 ± 4.1 mmol $O_2$ $m^{-3}$ $d^{-1}$, respectively; $F = 15.32$, $p < 0.0001$). The lowest, negative, NCP was measured in the dark period in late fall–early winter 2006 (average ± SE = -0.8 ± 0.3 mmol $O_2$ $m^{-3}$ $d^{-1}$, Table 2, Fig. 3). In summer NCP tended to be negative, indicative heterotrophic communities prevailing in this season. Most summer stations supported plankton communities in a post-bloom stage, when the CR of the planktonic community exceeds production, being supported by the surplus production derived from the bloom period. Consistently, in summer oxygen content tended to be undersaturated (mean ± SE = 89.30 ± 0.88). NCP values differed with water masses ($F = 4.58$, $p < 0.02$), with communities sampled in Atlantic water having statistically significant higher values (mean ± SE = 11.1 ± 1.7) than in warmed Polar Surface waters (mean ± SE = 3.2 ± 2.0 mmol $O_2$ $m^{-3}$ $d^{-1}$), but comparable to those sampled in Polar surface waters (mean ± SE = 7.0 ± 1.7, Figure 4). NCP also differed significantly among regions ($F = 9.32$, $p < 0.0001$), with the East Fram Strait having higher NCP values (mean ± SE = 44.5 ± 7.5 mmol $O_2$ $m^{-3}$ $d^{-1}$) than the other sampled areas.

Gross Primary Production (GPP) varied from absence of photosynthetic activity (i.e. GPP = 0) in the cruise conducted during the dark period (late fall-early winter 2006) and values of 0 at 30 m depth waters sampled in summer 2007, to a maximum value of 80.0 ± 1.7 mmol $O_2$

$m^{-3}$ $d^{-1}$ recorded in spring 2011 at 15.2 m depth in Kongsfjorden (Table S1). GPP values differed among cruises ($F = 15.50$, $p < 0.0001$, Table 2, Fig. 3), with the spring cruises of 2010 and 2011 having much higher values than the other cruises (mean ± SE = 25.8 ± 3.4 and 24.8 ± 3.7 mmol $O_2$ $m^{-3}$ $d^{-1}$, respectively). Gross primary production differed between water masses ($F = 4.88$, $p < 0.009$), with AW having significantly higher GPP (mean ± SE =14.5 ± 1.9 mmol $O_2$ $m^{-3}$ $d^{-1}$) than PSWw (mean ± SE = 6.3 ± 1.0 mmol $O_2$ $m^{-3}$ $d^{-1}$), but comparable to PSW (mean ± SE = 13.0 ± 2.5 mmol $O_2$ $m^{-3}$ $d^{-1}$, Fig 4). GPP also differed between sampled areas ($F = 7.67$, $p < 0.0001$), with the East Fram Strait, the Barents Sea and Svalbard Fjords having statistically significant higher values than the other areas.

Community Respiration (CR) varied from a minimum value of 0.0 ± 0.4 mmol $O_2$ $m^{-3}$ $d^{-1}$ measured in spring 2007 to 40.9 ± 0.6 mmol $O_2$ $m^{-3}$ $d^{-1}$ measured in spring 2011. The respiration rates were similar among cruises, although the respiration rate in the spring 2011 cruise was significantly higher (mean ± SE = 7.2 ± 1.6 mmol $O_2$ $m^{-3}$ $d^{-1}$) than that measured during the summer of 2008 and that measured in spring 2010 ($F = 3.76$, $p < 0.001$; Fig. 3). CR did not show statistically significant differences between water masses ($F = 0.16$, $p = 0.85$) or between sampled areas ($F = 1.86$, $p = 0.08$). CR varied greatly, over 2 orders of magnitude, between stations from the same cruise in four of the eight cruises (Table 2). This high variability between stations sampled in the same cruise masks any existing seasonal variability in respiration rates. There was not significant relationships ($p > 0.05$) between metabolic rates and nutrient concentrations.

The ratio of GPP to CR (GPP/CR) describes the metabolic status of the community, which is net heterotrophic when GPP/CR < 1, net autotrophic when GPP/CR < 1 or in metabolic balance when GPP/CR = 1 (i.e. GPP = CR). GPP/CR varied between 0, for the late fall–early winter cruise in the dark, when no primary production occurred, to a very high value of 549.7 measured at 15 m depth in the Barents Sea in spring 2010, the highest value reported. There were significant differences in the GPP/R ratio between cruises (ANOVA, $F = 3.19$, $p < 0.004$), with the cruise in spring 2010 having the highest GPP/R ratio (mean ± SE = 49.53 ± 25.65), indicative of the overwhelming dominance of autotrophic production characteristic of the spring bloom stage (Fig. 3). GPP/CR did not show statistically significant differences between water masses ($F = 1.33$, $p > 0.05$) or between sampling areas ($F = 1.73$, $p > 0.05$).

The ratio of NCP to GPP (NCP/GPP) can be considered an estimate of f-ratios, the fraction of total primary production supported by nitrate (Quinones and Platt 1991). On a long-term basis

and with the assumption of steady state, NCP can be considered equal to export production (Eppley and Peterson 1979), as the storage in the upper water column is small relative to the production rates. However, the assumption that NCP equals export production fails when NCP is negative. When respiration exceeds production and the community is heterotrophic export should be supported by organic matter produced in a recent time period, advected from neighboring waters or allochthonous inputs. NCP/GPP varied between -78.95 and 1, with a mean value of -0.67 ± 0.55. There was no statistically significant difference in NCP/GPP between cruises, seasons, water masses or sampled areas.

During the cruise conducted in summer 2008 CR increased linearly with GPP as described by the fitted regression equation: CR = 0.52 + 0.62 (± 0.13) GPP ($R^2 = 0.54$, $p < 0.0001$, N = 22), but no such relationship was found for the other cruises. For the entire data set there was a weak, albeit significant relationship between CR and GPP as described by the fitted regression equation: CR = 3.29 + 0.08 (± 0.03) GPP ($R^2 = 0.04$, $p < 0.01$, N = 165). There was also a weak, albeit significant relationship between CR and DOC and Bacterial Abundance (AB), described by the fitted regression equations: log CR = -10.37 (± 3.69) + 2.50 (± 0.82) log DOC (μM) ($R^2 = 0.19$, $p < 0.005$, N = 41) and log CR = -3.15 (± 2.13) + 0.31 (± 0.16) log BA ($R^2 = 0.06$, $p < 0.05$, N = 64).

The GPP/CR ratio increased significantly with GPP as described by the fitted ordinary least squares regression equation:

log GPP/CR = -0.37 + 0.78 (± 0.07) log GPP ($R^2 = 0.53$, $p < 0.0001$, N = 112);

and by the fitted model II regression equation:

log GPP/CR = -0.63 + 1.08 log GPP ($p < 0.05$, N = 112)

NCP increased significantly with GPP as described by the fitted ordinary least squares regression equation,

NCP = -4.61 + 0.97 (± 0.04) GPP ($R^2 = 0.91$, $p < 0.0001$, N = 78),

and by the fitted model II regression equation:

NCP = -5.31 + 1.02 GPP ($p < 0.05$, N = 78)

Community respiration rates increased with increasing gross primary production as described by the fitted logistic regression equation:

Log CR (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 0.37 (± 0.07) + 0.22 (± 0.07) log GPP (mmol $O_2$ $m^{-3}$ $d^{-1}$)

411 ($R^2 = 0.08$, $p < 0.005$ n = 112), where the slope is significantly < 1 ($p < 0.0001$) indicating
412 that community respiration is highest relative to GPP in communities with low GPP.

413 Both volumetric and integrated NCP and GPP tended to decrease with increasing
414 temperature. Examination of the relationship between production rates (both NCP and GPP)
415 and temperature showed that the range of production rates become narrower with increasing
416 temperature, with most production rates being low at higher temperatures (Fig. 5).
417 Conversely, volumetric and integrated CR tended to increase with increasing temperatures,
418 with the range of respiration rates becoming wider with increasing temperature (Fig. 5).

419 There was also positive relationship between GPP and Chlorophyll *a* for the stations and
420 cruises where the data were available (Figure 6).

421 **3.2.2 Integrated metabolic rates**

422 Depth-integrated metabolic rates, integrated down to 20 m, were calculated for each station
423 (Table 2). Integrated NCP ranged broadly from -251.6 to 1065.5 mmol $O_2$ $m^{-2}$ $d^{-1}$. The lowest
424 value was measured in the central Fram Strait during summer 2007, whereas the higher was
425 measured in the Kongsfjorden during spring 2011 (Table 2). The minimum integrated GPP
426 was 0 mmol $O_2$ $m^{-2}$ $d^{-1}$ during the late fall-early winter cruise, conducted under 24 h of
427 darkness, and the maximum integrated GPP was 1073.1 mmol $O_2$ $m^{-2}$ $d^{-1}$ measured in the
428 Kongsfjorden during the spring cruise in 2011 (Table 2). The minimum integrated CR rate
429 (0.35 mmol $O_2$ $m^{-2}$ $d^{-1}$) was measured in the Barents Sea during the late fall-early winter
430 cruise and the maximum (475.8 mmol $O_2$ $m^{-2}$ $d^{-1}$) in the central Fram Strait during summer
431 2007 (Table 3). Depth-integrated metabolic rates were also calculated for an integration depth
432 of 30m where data were available (Table S2). There were no significant differences between
433 the metabolic rates integrated to 20 or 30 m depth ($p > 0.05$).

434 In late fall–early winter cruise, in absence of light, all stations supported net heterotrophic
435 communities. In spring, at the onset of the 24 h daylight period, communities are expected to
436 be strongly autotrophic. Indeed, all stations had net autotrophic communities in early spring
437 2007, but the community at one of the three stations sampled in 2008 was net heterotrophic.
438 The extreme low temperature and heavy ice cover encountered during early spring did not
439 yield the appropriate conditions for bloom development. In May all stations were net
440 autotrophic and the GPP/CR ratio was very high, with great production and low respiration
441 rates, indicative of a bloom development. In the late spring-early summer cruise conducted in
442 2009 one of the eight sampled stations were found to be net heterotrophic. In the summer

443 cruises a total of 40 % (N = 22) and 33 % (N = 7) of the stations were found to support net
444 heterotrophic communities in 2007 and 2008 respectively.

445

446 ## 4. Discussion

447 ### *4.1. Methods used*

448 The Winkler method estimates planktonic metabolism in closed systems and it is subject to
449 possible 'bottle effects'. The mysterious 'bottle effect' refers to the concern that phenomena
450 observed in confined assemblages derive from the consequences of the confinement of the
451 community and could be different than under natural conditions (Pernthaler and Amann 2005;
452 Hammes et al. 2010). Some of the artefacts derived from bottle incubation are produced by
453 substrates and bacteria adsorption and bacterial proliferation on glass surface. Long
454 incubation periods can also imply modifications in bacterial activity and diversity (Massana
455 et al. 2001). However, several authors did not find any difference in microbial metabolism
456 and/or growth (Fogg and Calvariomartinez 1989; Hammes et al. 2010; Garcia-Martin et al.
457 2011) when using different bottle sizes, which is one of the components determining the
458 "bottle effect", when existing. Thus, although structural changes may occur, the metabolic
459 rates measured through incubation bottles are considered to be meaningful (Gasol et al.
460 2008).

461 Alternative methods to estimate planktonic metabolism, avoiding 'bottle effects' include the
462 assessment of the biological $O_2$ saturation, which refers to the differences between $O_2$ and Ar
463 saturation (Quay et al. 1993), and the triple oxygen isotope composition ($^{16}O$, $^{17}O$, and $^{18}O$) of
464 dissolved $O_2$ (Luz and Barkan 2000). $O_2$/Ar gas ratios measured in situ can be combined with
465 the oxygen triple isotope composition to estimate rates of NCP (Bender 2000; Hendricks et
466 al. 2004; Reuer et al. 2007). The combination of these methods to estimate community
467 metabolism remove the 'bottle effect' and integrate metabolic rates over period of weeks to
468 months, but has a high associated error, from 30 to 40% (Juranek and Quay 2005; Robinson
469 and Williams 2005).

470 Estimation of NCP in the upper water column can also be made from direct analysis of
471 decreases in total dissolved inorganic carbon (DIC) after correcting for $CO_2$ exchange with
472 the atmosphere (Ishii et al., 1998).

## 4.2. Metabolic rates

There is a remarkable paucity of direct measurements of planktonic metabolic rates in the Arctic Ocean, with most available studies reporting only one of the components involved in the assessment of metabolic balance (Table 3) or deriving metabolic rates from models. The rates reported in this study are within the rates reported in the past, except for the NCP we report for the winter, which is the only negative rate so far reported (Table 3), as NCP had not been assessed for Arctic communities in winter in the past, and for the GPP values reported for the spring 2010, well above previous estimates reported for the Arctic Ocean.

Planktonic metabolism in the Arctic Ocean margins exhibits, as expected, important annual variability, which is compounded with considerable spatial variability, partially masking the seasonal signal. The absence of sunlight and photosynthetic activity in winter renders Arctic planktonic communities heterotrophic, consuming the excess dissolved organic matter produced during the light period of the year and acting as $CO_2$ sources in winter. The productive photic period may generate dissolved organic matter (DOM) slow-to-degrade, which could support bacterial production during winter, as it has been demonstrated in Antarctic waters (Azam et al. 1991; Azam et al. 1994). We examined whether the DOC pool is sufficient to subsidize winter respiration, when darkness prevents the inputs of fresh photosynthetic period. We estimated, using the respiration rate measured in winter (Table 2), the respiratory carbon demand to be 75.26 ± 100.35 μmol $L^{-1}$ during the dark period. This is below the average DOC pool in the area studied (89.01 ± 2.46 μmol C $L^{-1}$, Kritzberg et al. 2010, Tovar-Sánchez et al. 2010 and this study), suggesting that the large DOC pool in Arctic waters would suffice to maintain significant respiration rates in the plankton community across the dark period assuming all this DOC was labile. However, the resulting DOC concentration would be below that ever recorded in the ocean. Hence, respiration rates in the plankton community across the dark period must be supported by allochthonous DOC inputs. During the dark period the West Spitsbergen Current transports warm Atlantic Water (AW) northward melting ice and maintaining open the waters west of Svalbard. This Atlantic water transports important amounts of DOC that can be used to support bacterial respiration during the dark period.

Spring, with the increase in PAR and the onset of melting of seasonal ice and surplus nutrients, is the most productive time of the year, when algal blooms occur (mainly in May) (Table 2). The highest NCP and GPP are both reached in spring (in a bloom stage), when

505 water temperatures remain low and ice cover is reduced (Table 2), with an extremely high
506 GPP/CR ratio, indicative of a spring bloom development, when production increases sharply
507 and respiration rates remain low. In a previous study, (Cottrell et al. 2006) also reported
508 higher metabolic rates in spring than in summer, but their production values were lower than
509 the values reported here (Table 3). These differences can be attributed to differences in the
510 stage of the bloom when the spring sampling was made. Whereas our spring samples were
511 taken in bloom situation (in May), the Cottrell et al. (2006) samples where probably taken
512 during a post-bloom situation, as their GPP/CR ratios are lower than those measured here.
513 The spring bloom in Arctic water can account for a 40% of the total annual primary
514 production (Lavoie et al. 2009). In addition, our study was conducted mainly in the Fram
515 Strait, whereas their study was conducted in the Chukchi Sea, at lower latitude than our study
516 area, which may affects seasonal development.

517 NCP and GPP tended to decrease with increasing temperatures, concurrent with recent
518 experimental work (Holding et al. 2012). At low temperatures high GPP and NCP are reached
519 during the spring bloom, and low GPP and NCP at stages previous to the development of the
520 bloom. Thus, at low temperatures we found a high variability of NCP and GPP data (Figure
521 5), whereas at higher temperatures these metabolic rates tended to decrease and variability is
522 lower. This suggests that the NCP and GPP are related to the stage of the bloom at lower
523 temperatures, while at higher temperatures temperature dependence controls the relationship.

524 The GPP observed during the summer cruise in 2007 (the only cruise where all necessary
525 data were available) was compared with the upper limit imposed by the underwater PAR, the
526 light absorbed, calculated from chlorophyll a using the specific absorption coefficient for
527 Arctic communities by Matsuoka et al. 2009, and the quantum yield (from Kirk 1983). The
528 results indicated that the observed GPP represents, on average, 4.6 ± 1.3 % of the maximum
529 possible rates, and a maximum observed value of 57.8 % in one of the stations. GPP for the
530 spring bloom is expected to approach more closely the biophysical maximum imposed by
531 light and the quantum yield. Unfortunately, we lack the data needed to make comparable
532 calculations.

533 The GPP/CR ratio increased with increasing GPP, as observed elsewhere in the ocean (see
534 Duarte and Agusti 1998, Duarte and Regaudie-de-Gioux 2009), implying that unproductive
535 Arctic communities tend to have a low GPP/CR, thus tending to be heterotrophic. The fitted
536 regression equation implies that the average GPP required to balance Arctic planktonic

metabolism is 3.01 mmol $O_2$ $m^{-3}$ $d^{-1}$, when using ordinary least squares (OLS) regression and of 3.82 mmol $O_2$ $m^{-3}$ $d^{-1}$ when using model II regression. Fitting the relationship between Log CR and Log GPP using a logistic regression yields exactly the same result 3.01 mmol $O_2$ $m^{-3}$ $d^{-1}$ as that obtained using ordinary least squares regression. However, use of the relationship between NCP and GPP to derive the GPP required to metabolic balance (i.e. GPP at NCP = 0) yields a higher value of 4.78 mmol $O_2$ $m^{-3}$ $d^{-1}$, when using OLS regression and of 5.22 mmol $O_2$ $m^{-3}$ $d^{-1}$when using model II regression. These rates are higher than average rates for oceanic communities (1.07 mmol $O_2$ $m^{-3}$ $d^{-1}$), but lower than a previously reported value for the Arctic Ocean based on a more limited data set collected in summer (5.45 mmol $O_2$ $m^{-3}$ $d^{-1}$, Duarte and Regaudie-de-Gioux 2009).

Although by definition f-ratios cannot be negative, NCP/GPP was negative in most stations, as heterotrophic conditions prevailed in most stations. So, the assumption that NCP/GPP is an estimate of f-ratio does not apply when respiration rates exceed production. Long-term sediment traps always measure positive vertical flux, although very low in Polar areas during winter (Lalande et al, 2009), when heterotrophic conditions prevail. The exported material may originate from heterotrophic community or the present POC pool accumulated last year. The settling material is export of accumulated material from earlier PP, a pool of organic material that may have been recycled several times in the upper layers (Wassmann et al. 1998), or been advected to the area - not the in-situ production on a day to day basis. Forest et al. (2010) found a delay between PP and Vertical carbon export of 55-90 days in the Fram Strait.

Pelagic respiration in the Arctic may be subsidised by riverine inputs of organic carbon, as the Arctic receives the discharge of some of the world's largest rivers, delivering 30 $10^6$ t C $yr^{-1}$ of organic carbon to the Arctic Ocean (Rachold et al. 2004), as a consequence the Arctic Ocean supports the highest concentration of terrestrial DOM in any ocean (Benner et al. 2005). There are also considerable inputs of allochthonous organic matter with the AW flowing to the North (Wassmann 2001). Use of terrestrial DOM by marine bacterial communities will largely depend on its chemical composition and lability (Sondergaard et al. 2003). Glaciers can be a considerable source of labile organic matter to the marine environment in the Gulf of Alaska, with 66% of the total DOC being bioavailable (Hood et al. 2009). This study reported bioavailable DOC to range between the 23 and 66% in different watersheds of the Gulf of Alaska.

569 Although, diatoms are expected to represent an important component of the phytoplankton
570 community in the marginal ice zone and in waters influenced by ice melting (Von Quillfeldt
571 1997, 2000; Falk-Petersen et al. 1998), during our summer cruise in 2007, the
572 prymnesiophyte *Phaeocystis pouchetti* in its colonial form dominated the phytoplankton
573 community and diatoms represented only 7.3 % of the phytoplankton biovolume (Lasternas et
574 al. 2010). In the only station where diatom abundance exceeded that of *P. pouchetti* the
575 lowest NCP and the highest CR rates were measured (in this station the water temperature
576 was the warmest measured in the cruise). Diatoms were found to be scarce in colder and low
577 salinity waters, indicating that this group was more affected by ice melting (Lasternas et al.
578 2010). During the spring cruise in 2008, the phototrophic protist biomass dominated over that
579 of heterotrophic protists in the stations with autotrophic metabolism, suggesting that protists
580 strongly contributed to the metabolism of the communities (Seuthe et al. 2011). In contrast,
581 bacterial respiration appeared to be small during this cruise, as indicated by very low rates of
582 bacterial production (Seuthe et al. 2011). During the pre-bloom stage, in heavily ice-covered
583 waters, protists are believed to greatly contribute to community metabolism (Seuthe et al.
584 2011).

585 An approximation to the annual metabolic rates in the western European Arctic sector can be
586 attempted with the integrated metabolic rates presented here. However, this exercise must be
587 considered a tentative one, due to the sparse sample density over time, particularly during
588 wintertime and transition periods between polar night and midnight sun. The mean annual
589 GPP was calculated to be 32 mol $O_2$ $m^{-2}$ $year^{-1}$ (305 g C $m^{-2}$ $year^{-1}$) and the mean annual CR
590 was estimated at 20 mol $O_2$ $m^{-2}$ $year^{-1}$ (197 g C $m^{-2}$ $year^{-1}$), lower than the GPP estimate.
591 Accordingly, these calculations indicate that the mean annual NCP (NCP = GPP – CR) across
592 the study area is expected to be positive at 11 mol $O_2$ $m^{-2}$ $year^{-1}$ (108 g C $m^{-2}$ $year^{-1}$), implying
593 that the planktonic community in the European sector of the Arctic is likely to be net
594 autotrophic at the annual scale, thereby acting as a significant atmospheric carbon sink. The
595 spring bloom, with a duration of 14 days contributed to the 26% of the total annual gross
596 primary production. The GPP estimate reported here is a 69% higher than previous estimates
597 of annual production for this area (average of 93 ± 18 g C $m^{-2}$ $year^{-1}$, Wassmann et al, 2006b).
598 The annual NCP value derived here is slightly lower than NPP values derived from satellite-
599 data for the Bering Sea (124 g C $m^{-2}$ $year^{-1}$), and bellow the global mean of 140 g C $m^{-2}$ $year^{-1}$
600 (Brown et al. 2011).

An increased sampling frequency will be required to improve these estimates; an effort that will require increased international collaboration. While there is ample room for improvement, the annual estimate derived here for the studied region is based on a sampling effort unparalleled for any other polar region (Robinson and Williams 2005), where plankton metabolism remains grossly under-sampled.

The estimate provided here does not include production by ice algae, generally reported to contribute 5-10% of overall primary production in shelf areas (Horner and Schrader 1982; Gosselin et al. 1997; Lavoie et al. 2009) or microbial respiration in sea ice, that has been shown to be an important organic C sink in sea ice (Nguyen and Maranger 2011). Ice algae production has been reported at an average of 36 mg C $m^{-2}$ $d^{-1}$ in the Beaufort Sea with a peak of 62 mg C $m^{-2}$ $d^{-1}$ in May (Horner and Schrader 1982), at 28 mg C $m^{-2}$ $d^{-1}$ in the Chuckchi Sea (Gosselin et al. 1997) and at 14.5 mg C $m^{-2}$ $d^{-1}$ in the northern Barents Sea (Hegseth 1998). The estimate provided here does not include zooplankton respiration rates, estimated to have requirements in the upper 200 m in summer of 2007 averaging 23.2% of the $^{14}C$ primary production (Alcaraz et al. 2010).

Previous studies reported an increase of Arctic primary production in recent years. (Arrigo et al. 2008) estimated that the net annual $CO_2$-fixation by Arctic plankton has increased by 26% (6.5 % per year) between 2003 and 2007, and Pabi et al. (2008) reported a 30% increase in Arctic annual primary production between 1998 and 2006. This trend is expected to continue. However, close inspection of the data presented by Arrigo et al. (2008) shows that the primary production in the Atlantic sector of the Arctic Ocean did not increase in the summer of 2007. As the Artic Ocean is very heterogeneous and exhibits a wide range of regional responses, responses to global warming will probably also vary across regions. Ellingsen et al. (2008) predict an increase of primary production in the Barents Sea of 8% over the period 1995-2059. These studies support their statements on the predictions of ice melting and reduced ice surface, leading to an extended productive season.

Yet, respiration rates are also expected to increase with increasing temperature, more so than primary production (Harris et al. 2006; Lopez-Urrutia et al. 2006). In the studied area community respiration rates are predicted to increase by 62% with a 6 ºC warming (Vaquer-Sunyer et al. 2010), doubling the 30% increment expected for primary production (Wassmann et al. 2008). Bacterial respiration is also predicted to increase faster than bacterial production in this area (Kritzberg et al. 2010). Thus the net community production may not increase or

633 may even decrease in the future. Warming can result in weakening substantially the role of
634 Arctic communities as significant CO2 sinks and may even be reverted to become $CO_2$
635 sources to the atmosphere (Vaquer-Sunyer and Duarte, 2010) because warming is predicted
636 to increase the carbon flow through bacteria and that most of the carbon consumed would be
637 released as $CO_2$ (Kritzberg et al. 2010). Indeed, a recent experimental assessment suggests the
638 existence of a 5ºC threshold for Arctic waters, beyond which the metabolism (NCP) of
639 plankton communities shifts from autotrophic to heterotrophic (Holding et al. 2011). This
640 study also finds a similar threshold response where community respiration doubles at 5ºC
641 concurrent with previous work (Vaquer-Suyner et al. 2010). Rising temperature also affects
642 ice melting, thereby also affecting the production of ice algae, and increases river discharge
643 (Peterson et al. 2002), which may lead to higher DOC inputs the Arctic Ocean (Cooper et al.
644 2005), possibly supporting higher pelagic respiration rates.

645 Ice melting can also produce a decrease in primary production (Regaudie-De-Gioux and
646 Duarte 2010; Duarte et al. Submitted), consistent with the positive relationship between
647 Chlorophyll a and salinity and the negative relationship between production rates and
648 temperature reported here. These results are in contrast with earlier findings for the Southern
649 Ocean that suggest that freshwater discharge with ice melting should increase primary
650 production due to increased stratification (Montes-Hugo et al. 2009; Montes-Hugo et al.
651 2010).

652 Global warming results in an 'atlantification' of large regions in the Atlantic sector of the
653 Arctic Ocean (Wassmann et al. 2004). Implications of 'atlantifications' will be multiple,
654 affecting vertical mixing and introducing Atlantic species that competitively displace Arctic
655 species poleward, among others. However, the effects of "atlantification" of the Arctic
656 metabolic rates are unknown. As atlantification is expected to reduce stratification, it will
657 result in significant changes in phytoplankton composition, bloom size and development, and
658 vertical flux possibly leading to a regime shift in the Arctic marine ecosystem (Wassmann et
659 al. 2004).

660 The results presented here provide a first assessment of seasonal and spatial variability in
661 planktonic metabolism in the Western European sector of the Arctic, allowing the evaluation
662 of patterns in metabolic rates and a first, albeit rough, approximation of the annual metabolic
663 balance of Arctic plankton communities. The estimates derived here can be improved further
664 through efforts to resolve spatial variability in Arctic metabolic rates and increasing the

research effort during fall and winter, when harsh weather conditions render oceanographic research in the high Arctic cumbersome. Particular efforts are required to capture the metabolic rates during the onset and subsequent development of the highly seasonal spring bloom period, which may last for only two weeks in marginal ice zones (Wassmann et al. 2006a, 2006b). The results provided here have an important value as a necessary baseline to assess future changes in plankton metabolism with warming and ice loss in the Arctic, which can affect the role of the Arctic Ocean in a warmer Earth System.

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999 Figure legends:

1000 Figure 1. Map showing the location of the stations sampled along the 5 cruises covering the
1001 northern Fram Strait, Spitsbergen waters and the western Barents Sea. Arrows indicate the
1002 direction of the main currents present in the area, the West Spitsbergen Current (WSC, thin
1003 black arrows) and the East Greenland Current (EGC, thick grey arrows).

1004 Figure 2. Mean (± SE) surface seawater temperature (ºC, circles) and Chlorophyll a (µg Chl *a*
1005 $l^{-1}$) concentration (triangles) over time.

1006 Figure 3. Box plots showing the distribution of metabolic rates for the different cruises
1007 presented here: (A) Net community production (NCP), (B) Gross primary production (GPP),
1008 (C) Community respiration (CR) rates and (D) the ratio of GPP to CR. All rates reported in
1009 mmol $O_2$ $m^{-3}$ $d^{-1}$. The boxes show the median of the metabolic rates plus the lower (25%) and
1010 upper (75%) quartiles, the whiskers indicate 1.5 times the Interquartile Range (IQR). Letters
1011 indicate the results for a Tukey HSD-test, whereby the metabolic rate did not differ
1012 significantly for cruises with the same letter.

1013 Figure 4. Box plots showing the distribution of metabolic rates for the different water masses
1014 sampled here: (A) Net community production (NCP), (B) Gross primary production (GPP),
1015 (C) Community respiration (CR) rates and (D) the ratio of GPP to CR. All rates reported in
1016 mmol $O_2$ $m^{-3}$ $d^{-1}$. The boxes show the median of the metabolic rates plus the lower (25%) and
1017 upper (75%) quartiles, the whiskers indicate 1.5 times the Interquartile Range (IQR). Letters
1018 indicate the results for a Tukey HSD-test, whereby the metabolic rate did not differ
1019 significantly for water masses with the same letter.

1020 Figure 5. Relationship between volumetric and integrated metabolic rates and water
1021 temperature: (A) volumetric net community production (NCP), (B) volumetric gross primary
1022 production (GPP), (C) volumetric community respiration (CR), (D) integrated NCP, (E)
1023 integrated GPP and (F) integrated CR. Solid lines represents the fitted regression for the
1024 median or the 50% quartile [(A) NCP (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 2.28 (± 1.04) – 0.31 (± 0.25)
1025 Temperature (ºC), N = 201, p = 0.21); (B) GPP (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 6.57 (± 1.43) – 0.22 (±
1026 0.26) Temperature (ºC), N = 167, p = 0.40); (C) CR (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 2.10 (± 0.24) + 0.13
1027 (± 0.08) Temperature (ºC), N = 167, p = 0.07); (D) NCP (mmol $O_2$ $m^{-2}$ $d^{-1}$) = 63.75 (± 40.75)
1028 – 13.87 (± 8.69) Temperature (ºC), N = 58, p = 0.12); (E) GPP (mmol $O_2$ $m^{-2}$ $d^{-1}$) = 228.23 (±
1029 45.54) – 33.76 (± 9.46) Temperature (ºC), N = 48, p < 0.001); (F) CR (mmol $O_2$ $m^{-2}$ $d^{-1}$) =
1030 36.68 (± 11.34) + 5.01 (± 5.52) Temperature (ºC), N = 47, p = 0.37) ]. Dashed lines represent

1031 the fitted regression for the 90% quantile [(A) NCP (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 30.98 (± 4.99) – 4.63
1032 (± 1.23) Temperature (ºC), N = 202, $p < 0.0005$; (B) GPP (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 35.41 (± 5.66)
1033 – 4.06 (± 1.50) Temperature (ºC), N = 168, $p < 0.01$; (C) CR (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 9.18 (±
1034 1.16) + 0.72 (± 0.48) Temperature (ºC), N = 168, $p = 0.14$; (D) NCP (mmol $O_2$ $m^{-2}$ $d^{-1}$) =
1035 534.87 (± 164.28) – 79.88 (± 39.13) Temperature (ºC), N = 58, $p < 0.05$); (E) GPP (mmol $O_2$
1036 $m^{-2}$ $d^{-1}$) = 665.95 (± 173.15) – 63.19 (± 42.28) Temperature (ºC), N = 47, $p = 0.14$; (F) CR
1037 (mmol $O_2$ $m^{-2}$ $d^{-1}$) = 197.62 (± 30.36) + 4.85 (± 14.91) Temperature (ºC), N = 48, $p = 0.74$)]
1038 and the 10% quantile [(A) NCP (mmol $O_2$ $m^{-3}$ $d^{-1}$) = -2.27 (± 1.07) – 0.72 (± 0.54)
1039 Temperature (ºC), N = 202, $p = 0.18$; (B) GPP (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 0.66 (± 0.28) – 0.03 (±
1040 0.09) Temperature (ºC), N = 168, $p = 0.74$; (C) CR (mmol $O_2$ $m^{-3}$ $d^{-1}$) = 0.56 (± 0.13) + 0.01
1041 (± 0.05) Temperature (ºC), N = 168, $p = 0.84$; (D) NCP (mmol $O_2$ $m^{-2}$ $d^{-1}$) = -21.85 (± 31.56)
1042 – 13.00 (± 14.58) Temperature (ºC), N = 58, $p = 0.38$; (E) GPP (mmol $O_2$ $m^{-2}$ $d^{-1}$) = 3.32 (±
1043 6.46) – 0.69 (±0.96) Temperature (ºC), N = 48, $p = 0.48$; (F) CR (mmol $O_2$ $m^{-2}$ $d^{-1}$) = 14.02 (±
1044 4.17) – 1.70 (± 0.92) Temperature (ºC), N = 47, $p = 0.07$].

1045 Figure 6. The relationship between Gross primary production (GPP) and chlorophyll *a*
1046 concentration. The solid line shows the fitted regression equation GPP (mmol $O_2$ $m^{-3}$ $d^{-1}$) =
1047 0.30 + 2.26 (± 0.29) Chl a (µg Chl *a* $l^{-1}$) ($R^2 = 0.38$, $p < 0.0001$, N = 98).
1048

1049 Table 1. Summary of water temperature (ºC), Salinity (psu) and chlorophyll a content average
1050 (± SE, derived from the variance of the values used to calculate the mean) and range, and the
1051 corresponding ice conditions for the different cruises and different sampled areas (and
1052 number of stations sampled at each area) for the depths where metabolism was assessed.
1053

| Cruise | Dates | Study area (number of stations) | Number of Stations | Water temperature (ºC) | Salinity (psu) | Chlorophyll a | Ice conditions |
|---|---|---|---|---|---|---|---|
| ARCTOS | 29/11/2006-30/11/2006 | Barents Sea | 2 | 5.9 ± 0.8 (5.1 to 6.7) | 35.1 ± 0.0 (35.1 to 35.1) | nd | Open waters |
| | 01/12/2006 | Fram Strait | 1 | 4.8 ± 0 | 35.0 | nd | Open waters |
| | 02/12/2006-05/12/2006 | Kongsfjorden | 4 | 1.2 ± 0.3 (0.5 to 1.8) | 34.5 ± 0.1 (34.3 to 34.6) | 0.02 ± 0.02 | Open waters |
| iAOOS 07 | 16/04/2007-25/04/2007 | West Fram Strait | 4 | -1.8 ± 0.0 (-1.8 to -1.7) | 32.4 ± 0.4 (30.4 to 33.9) | 0.03 ± 0.00 (0.00 to 0.05) | Heavily ice-covered |
| ATOS | 01/07/2007-24/07/2007 | Fram Strait (8) North Spitsbergen (10) Greenlad Sea (4) | 22 | 2.4 ± 0.3 (-1.7 to 7.0) | 33.8 ± 0.1 (31.5 to 35.1) | 2.43 ± 0.24 (0.26 to 6.84) | Open waters - ice presence |
| iAOOS 08 | 24/04/2008-08/05/2008 | West Fram Strait (2) Greenland shelf (2) | 3 | -1.8 ± 0.01 (-1.8 to -1.7) | 32.8 ± 0.2 (31.9 to 33.8) | 0.11 ± 0.02 (0.01 to 0.21) | Heavily ice-covered |
| JM 08 | 30/07/2008-05/08/2008 | Fram Strait | 7 | 2.6 ± 0.4 (-1.1 to 5.5) | 33.8 ± 0.2 (31.3 to 35.0) | 2.11 ± 0.41 (0.47 to 9.50) | Open waters - ice presence |
| ATP 09 | 17/06/2009-27/06/2009 | Barents Sea (4) East Fram Strait (3) North Spitsbergen (1) | 8 | 0.8 ± 0.3 (-1.76 to 3.64) | 34.1 ± 0.1 (34.7 to 32.7) | 2.55 ± 0.22 (0.08 to 11.77) | Open waters - ice presence |
| ATP 10 | 05/05/2010-10/05/2010 | Barents Sea (5) East Fram Strait (1) Isfjord (1) | 7 | -0.4 ± 0.4 (-1.9 to 2.6) | 32.4 ± 0.4 (30.4 to 33.9) | nd | Open waters - ice presence |
| ATP 11 | 23/05/2011-03/06/2011 | Barents Sea (2) East Fram Strait (4) | 12 | 0.35 ± 0.27 (-1.6 to 4.1) | 34.4 ± 0.1 (33.7 to 35.1) | nd | |

Isfjord (2)

Kongsfjorden (1)

Van Mijenfjord (1)

North Spitsbergen (2)

Open waters

- ice presence

nd: no data

1056 Table 2. Mean, standard error, range and number of observations of volumetric (mmol $O_2$ $m^{-3}$
1057 $d^{-1}$) and median, standard error, range and number of observations (N) of integrated metabolic
1058 rates (mmol $O_2$ $m^{-2}$ $d^{-1}$).

1059

| | | ARCTOS | IAOOS 07 | ATOS | IAOOS 08 | JM 08 | ATP 09 | ATP 10 | ATP 11 |
|---|---|---|---|---|---|---|---|---|---|
| **volumetric** | | Fall/Winter 06 | Spring 07 | Summer 07 | Spring 08 | Summer 08 | Spring 09 | Spring 10 | Spring 11 |
| | **Mean** | -0.84 | 1.68 | 1.23 | 2.07 | 0.18 | 8.63 | 23.85 | 19.05 |
| | **SE** | 0.34 | 0.83 | 0.90 | 0.79 | 0.15 | 2.64 | 3.11 | 4.07 |
| **NCP** | **Minimum** | -2.56 | -0.58 | -21.72 | -1.11 | -1.55 | -1.91 | 1.37 | -13.28 |
| | **Maximum** | -0.02 | 10.96 | 22.71 | 8.46 | 1.75 | 62.49 | 47.61 | 81.64 |
| | **N** | 7 | 13 | 66 | 12 | 24 | 24 | 24 | 31 |
| | **Mean** | 0.84 | 0.78 | 5.28 | 1.18 | 1.72 | 3.21 | 2.45 | 7.24 |
| | **SE** | 0.34 | 0.38 | 0.71 | 0.27 | 0.20 | 0.51 | 1.07 | 1.63 |
| **CR** | **Minimum** | 0.02 | 0.01 | 0.24 | 0.12 | 0.17 | 0.80 | 0.07 | 0.41 |
| | **Maximum** | 2.56 | 1.73 | 29.20 | 1.72 | 3.22 | 9.89 | 23.02 | 40.91 |
| | **N** | 7 | 4 | 62 | 3 | 22 | 20 | 21 | 26 |
| | **Mean** | 0.00 | 0.75 | 6.02 | 1.11 | 1.95 | 12.90 | 25.77 | 24.57 |
| | **SE** | 0.34 | 0.38 | 0.69 | 0.53 | 0.24 | 3.06 | 3.41 | 3.66 |
| **GPP** | **Minimum** | | 0.29 | 0.05 | 0.12 | 0.24 | 0.59 | 1.52 | 3.27 |
| | **Maximum** | | 1.88 | 25.23 | 1.93 | 4.52 | 64.40 | 48.89 | 80.02 |
| | **N** | 7 | 4 | 62 | 3 | 22 | 20 | 21 | 31 |
| | **Mean** | | 7.76 | 2.00 | 0.94 | 1.61 | 5.99 | 49.53 | 5.55 |
| | **SE** | | 6.91 | 0.27 | 0.52 | 0.48 | 1.85 | 25.65 | 0.91 |
| **GPP/CR** | **Minimum** | | 0.45 | 0.01 | 0.14 | 0.28 | 0.67 | 1.7 | 0.43 |
| | **Maximum** | | 28.5 | 9.99 | 1.92 | 11.42 | 33.64 | 549.75 | 17.8 |
| | **N** | | 4 | 62 | 3 | 22 | 20 | 21 | 26 |
| | **Mean** | | -0.05 | -2.26 | -1.96 | -0.08 | 0.5 | 0.88 | 0.54 |
| | **SE** | | 0.45 | 1.37 | 2.05 | 0.17 | 0.1 | 0.03 | 0.11 |
| **NCP/GPP** | **Minimum** | | -1.21 | -78.95 | -6.03 | -2.63 | -0.49 | 0.41 | -1.31 |
| | **Maximum** | | 0.97 | 0.9 | 0.48 | 0.91 | 0.97 | 1 | 0.94 |
| | **N** | | 4 | 62 | 3 | 22 | 20 | 21 | 26 |
| **integrated** | | | | | | | | | |
| | **Median** | -10.87 | 13.99 | 8.00 | 35.10 | 3.73 | 154.60 | 469.63 | 359.00 |
| | **SE** | 8.06 | 28.09 | 46.41 | 33.51 | 4.69 | 44.87 | 156.11 | 149.32 |
| **NCP** | **Minimum** | -48.72 | 1.94 | -251.60 | -3.47 | -11.78 | -18.60 | 50.97 | -11.56 |
| | **Maximum** | -0.35 | 96.99 | 320.60 | 88.76 | 12.64 | 251.30 | 853.71 | 1065.00 |
| | **N** | 7 | 4 | 15 | 3 | 6 | 8 | 6 | 9 |
| | **Median** | 10.87 | 0.95 | 63.90 | 19.20 | 37.50 | 52.51 | 21.30 | 120.99 |
| | **SE** | 8.06 | | 41.44 | | 4.28 | 14.85 | 36.55 | 26.65 |
| **CR** | **Minimum** | 0.35 | | 9.25 | | 25.07 | 16.44 | 16.60 | 76.31 |
| | **Maximum** | 48.72 | | 475.78 | | 46.09 | 74.12 | 197.13 | 234.97 |
| | **N** | 7 | 1 | 14 | 1 | 6 | 5 | 6 | 7 |
| | **Median** | 0 | 4.54 | 124.88 | 18.12 | 45.62 | 230.42 | 453.67 | 351.90 |
| | **SE** | 0 | | 31.06 | | 9.90 | 45.35 | 123.78 | 150.67 |
| **GPP** | **Minimum** | 0 | | 17.26 | | 13.04 | 69.12 | 67.86 | 123.18 |
| | **Maximum** | 0 | | 382.49 | | 64.24 | 283.00 | 761.51 | 1073.14 |
| | **N** | 7 | 1 | 14 | 1 | 6 | 5 | 6 | 7 |
| | **Mean** | | 4.78 | 1.87 | 0.94 | 1.10 | 7.19 | 17.44 | 4.16 |
| | **SE** | | | 0.44 | | 0.16 | 2.85 | 5.96 | 1.43 |
| **GPP/CR** | **Minimum** | | | 0.36 | | 0.52 | 1.32 | 2.56 | 0.93 |
| | **Maximum** | | | 6.18 | | 1.72 | 14.20 | 37.76 | 9.88 |
| | **N** | | 1 | 14 | 1 | 6 | 5 | 6 | 7 |

1060 Table 3. Average planktonic metabolic rates (mmol $O_2$ $m^{-3}$ $d^{-1}$) for different studies of
1061 planktonic community metabolism in the Arctic Ocean. Rates given as gross primary
1062 production (GPP), net community production (NCP) and respiration (R). Number of
1063 measurements included for each rate is given (N).

| Authors | Region | Date | Season | GPP | NCP | CR |
|---|---|---|---|---|---|---|
| Cota, G.F., et al. 1996[a] | Chukchi Sea | 08/1993 | Summer | | 1.78 (37) | |
| Sherr and Sherr, 2003 | Canadian Basin | 19/10/1997-28/09/1998 | All | | | 0.55 (30) |
| Sherr and Sherr, 2003 | Canadian Basin | 09/07/1998-17/09/1998 | Summer | | | 1.07 (9) |
| Sherr and Sherr, 2003 | Canadian Basin | 28/03/1998-19/06/1998 | Spring | | | 0.29 (10) |
| Sherr and Sherr, 2003 | Canadian Basin | 27/12/1997-20/03/1998 | Winter | | | 0.19 (8) |
| Sherr and Sherr, 2003 | Canadian Basin | 27/11/1997, 12/12/1997 and 25/09/1998 | Autum | | | 0.79 (3) |
| Cottrell, M.T., et al. 2006[a] | Chukchi Sea | 07/94-07/96 | All | 5.74 (50) | 2.25 (110) | 3.01 (59) |
| Cottrell, M.T., et al. 2006[a] | Chukchi Sea | 07-08/2002 and 07-08/2004 | Summer | 5.41 (43) | 1.90 (93) | 2.51 (50) |
| Cottrell, M.T., et al. 2006[a] | Chukchi Sea | 05/2004 | Spring | 7.76 (7) | 4.14 (17) | 5.80 (9) |
| Cottrell, M.T., et al. 2006[a] | Chukchi Sea | 16/07/2002-26/08/2002 | Summer | 4.30 (29) | 1.90 (54) | 1.12 (35) |
| Cottrell, M.T., et al. 2006[a] | Chukchi Sea | 16/07/2004-26/08/2004 | Summer | 7.71 (14) | 1.90 (39) | 5.75 (15) |
| Hameedi, 1978[a] | Chukchi Sea | 07/1974 | Summer | 9.45 (42) | | |
| Apollonio, 1980 | Dumbell Bay | 09/07/1959 to 09/07/1959 | Summer | 3.17 (11) | 3.92 (11) | |
| Harrison et al. 1982 | Baffin Bay | 26/08/1978 to 21/09/1978 | Summer | 0.77 (14) | | |
| Olli et al. 2007[a] | Central Arctic | 26/07/2001 to 18/08/2001 | Summer | 0.63 (28) | | |
| This study | Fram Strait | 29/11/2006-10/05/2010 | All | 11.67 (170) | 7.44 (201) | 4.09 (167) |

| | | | | | | |
|---|---|---|---|---|---|---|
| This study | Fram Strait | 04/2007 and 04-05/2008 | Early Spring | 0.90 (7) | 1.87 (25) | 0.95 (7) |
| This study | Barents Sea | 06/2009 ,05/2010 and 05-06/2011 | Spring | 23.51 (62) | 19.16 (67) | 4.70 (58) |
| This study | Fram Strait | 07/2007 and 07-08/2008 | Summer | 5.53 (94) | 1.68 (102) | 4.18 (95) |
| This study | Fram Strait | 29/11/2006-05/12/2006 | Winter | 0.00 (7) | -0.84 (7) | 0.84 (7) |

[a]: data reported in carbon units converted to oxygen units assuming a 1.25 molar stoichiometry between $O_2$ and C (Williams et al. 1979).