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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 one in 2010 (spring). The results show that metabolisms 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 on 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 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$.

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 must 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 h 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.

The range of community metabolism expected in Arctic planktonic communities exceeds that for Antarctic waters, as the Arctic Ocean extends to much higher latitudes than the Southern Ocean does, involving more extreme transitions from complete darkness to continuous day light. 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, 2004; Wassmann et al., 2006; 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), 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 the methods used are the same and the area studied is in the same. 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). However, as integration depths vary between 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 as well as to ascertain the annual balance between gross primary production and plankton respiration in these communities. Whereas 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). 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.

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

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

2.2 Methods

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

Samples were collected in eight different cruises across five different periods of the year: the dark period in the late fall- early winter, early spring, spring, late spring–early summer, and summer (Table 1). One cruise was conducted in December, two in April, two in May, one in May–June, one in June, and two in July–August, respectively. Seven stations were sampled in December (Fig. 1, Table 1). Our two early-spring cruises were conducted in a pre-bloom situation, in heavily ice-covered waters on board the icebreaker KV *Svalbard*. Twenty-two stations were sampled in July 2007, eight in June 2009, seven in spring 2010 and twelve in spring 2011 (Fig. 1, Table 1).

Water samples were collected at different depths within the photic layer using a Rosette sampler system fitted with a CTD for a total of 70 stations, during the cruise conducted in April 2007 a 30 l GO-FLO or Niskin was used for 1 m samples. Samples were incubated for 48 h in December 2006 and in April 2007, when metabolic rates were particularly low, and for 24 h in the rest of cruises. Planktonic metabolism was evaluated from the changes in oxygen concentration in replicated (6 to 11 replicates, depending on season) narrow-mouth Winkler bottles. A set of bottles was fixed immediately to evaluate the initial oxygen content. The other sets of bottles were incubated in the light and the dark in water baths on deck at in situ temperature, using neutral screens to reduce incident irradiance and to mimic the light environment in situ during the summer cruises. In December 2006 the Winkler bottles were incubated for 48 h in the dark in a controlled temperature room inside R/V *Jan Mayen*, as there were 24 h of darkness at the time of sampling. In spring (April 2007 and 2008) incubations were conducted in situ, deploying a buoy from the deck of the ship and mooring it to the ice edge. Winkler bottles were attached to methacrylate supports and suspended at the same depth from which the samples had been sampled, thereby being exposed to the same light and temperature conditions. The work conditions were particularly challenging during the spring cruises, when low air temperatures (mean ± SE = $-13.1 \pm 0.3^{\circ}$C) lead to frequent and rapid freezing and breakage of Winkler bottles during exposure and retrieval.

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

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

Community Respiration rates (CR) were calculated from the difference between the initial oxygen concentration and the oxygen concentration in the dark bottles after incubation. Net Community Production (NCP) was calculated from the difference between the oxygen concentration in the clear bottles after incubation and the initial oxygen concentration. Gross Primary Production (GPP) was calculated as the sum of NCP and Respiration rates and standard errors using error propagation. All the rates are reported in mmol O_2 m^{-3} d^{-1}. This method assumes equal respiration rates in the light than in the dark. The assumption of equal respiration rates in bottles exposed to light and bottles incubated in the dark may lead to underestimate CR and GPP, because respiration rates are likely to be higher during daylight than during night (Grande et al., 1989; Pace and Prairie, 2005; Pringault et al., 2007), but do not affect NCP estimates (Cole et al., 2000). Metabolic rates were integrated down to 20 m. This depth was selected because it was sampled in most stations and it is close to the average depth of the chlorophyll maximum layer (mean ± SE = 23 ± 5 m), and since integration depths based on light penetration cannot be applied during the extended dark period.

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

Samples for dissolved organic carbon (DOC) were taken during the cruises conducted in summer 2007 and 2008. Dissolved organic carbon (DOC) measurements were performed on 10 ml water samples sealed in precombusted glass ampoules (450 °C 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.

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 °C, when these PSW are warmed and the temperature increases to higher temperatures than 0 °C these waters are called warmed Polar surface waters (PSWw); waters with a salinity higher than 34.4 and potential temperature above 2 °C 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.

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 included GPP is in both 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 threshold for metabolic balance free of this potential problem, was also used, based on inferring the GPP at NCP = 0 from the fitted relationship between NCP and GPP.

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

3 Results

The air temperature ranged from −25.2 °C in April 2007 to +7.95 in July 2007 and the seawater temperature varied from minimum values of −1.85 °C, recorded in spring 2007 on the East Greenland Shelf, to maximum values of 7 °C, recorded in summer 2007 in Atlantic waters (Table 1). The average seawater temperature was lowest for the two early-spring cruises (mean ±SE = −1.78 ± 0.01 °C in 2007 and in 2008) which took place in the Arctic Ocean outflow, followed by the other 3 spring cruises, and exceeded 2.4 °C for the other cruises (Table 1 and Fig. 2). These significant (ANOVA, $F = 16.72$, $p < 0.0001$) differences in water temperature between cruises can partly be attributed to seasonal differences but also to variability in the water masses sampled. Indeed, during early-spring cruises only Polar Surface Water (PSW) was sampled, whereas during the other five cruises Atlantic Water (AW) and warmed Polar Surface Water (PSWw) were also sampled. Differences in water temperature were also attributable to spatial differences, as there were significant differences in the temperature ($F = 11.02$, $p < 0.001$) among the various areas sampled (Barents Sea, North Spitsbergen, central Fram Strait, Svalbard Fjords, Greenland Sea, East Greenland Shelf and West Spitsbergen).

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

chlorophyll *a* concentrations at the stations and depths where metabolic rates were determined were lowest during late fall-early winter 2006 (0.02 ± 0.02 µg Chl *a* l^{-1}), somewhat higher in early spring (0.03 ± 0.00 µg Chl *a* l^{-1} in 2007 and 0.11 ±

$0.02\,\mu g\,Chl\,a\,l^{-1}$ in 2008), higher in summer ($2.43 \pm 0.24\,\mu g\,Chl\,a\,l^{-1}$ in 2007 and $2.11 \pm 0.34\,\mu g\,Chl\,a\,l^{-1}$ in 2008), and highest in spring 2009 ($2.55 \pm 0.22\,\mu g\,Chl\,a\,l^{-1}$, Table 1 and Fig. 2). Unfortunately, chlorophyll *a* analyses were not conducted for the cruises conducted in spring 2010 and 2011. Chlorophyll *a* content increased significantly with seawater salinity ($R^2 = 0.20$, $p < 0.0001$, $N = 122$) and seawater temperature ($R^2 = 0.08$, $p < 0.002$, $N = 122$) in the cruises and stations where data are available. Consequently, there were statistically significant differences in chlorophyll *a* concentration between water masses ($F = 6.55$, $p < 0.003$), with Atlantic water (mean ± SE = $2.90 \pm 0.41\,\mu g\,Chl\,a\,l^{-1}$) having significantly higher chlorophyll *a* content than Polar Surface Waters (PSW, mean ± SE = $1.25 \pm 0.31\,\mu g\,Chl\,a\,l^{-1}$), but comparable to warmed Polar Surface Water (PSWw, mean ± SE = $1.88 \pm 0.21\,\mu g\,Chl\,a\,l^{-1}$). This partly reflects the bloom stage sampled in the different regions. Unfortunately we do not have data available for the spring cruise in 2010 where apparently a 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 $132.65\,\mu mol\,C\,l^{-1}$ (Table 2). The average DOC concentration (mean ± SE = $89.01 \pm 2.46\,\mu mol\,C\,l^{-1}$) was comparable to that previously reported in the same area (Table 2).

The experimental standard errors (SE) among replicate samples varied between 0.04 and $6.27\,mmol\,O_2\,m^{-3}$, with a mean of $0.66 \pm 0.03\,mmol\,O_2\,m^{-3}$. These errors represent a mean of 0.19 % of the total value of the measurement, with the replicates of light bottles supporting a higher error than initial and dark bottles replicates. These errors are very close to the limit of analytical detection, reported to vary between 0.06 and $1\,mmol\,O_2\,m^{-3}$ (Robinson and Williams, 2005).

Net Community Production (NCP) ranged broadly from −21.7 ± 1.9 for strongly heterotrophic communities in summer 2007 to $81.6 \pm 0.7\,mmol\,O_2\,m^{-3}\,d^{-1}$ for strongly autotrophic communities in spring 2011 (Tables 3 and S1, Supplement).

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 3, 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, Fig. 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 3, 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 3). This high variability between stations sampled in the same cruise masks any existing seasonal variability in respiration rates. There was not significant relationship ($p > 0.05$) 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/CR ratio between cruises (ANOVA, $F = 3.19$, $p < 0.004$), with the cruise in spring 2010 having the highest GPP/CR 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), which is assumed to be related to export production (Eppley and Peterson, 1979). NCP can be considered equal to export production, 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 allochthonous C inputs. NCP/GPP varied between −78.95 and 1, with a mean value of −0.67 ± 0.55. By definition, f-ratios cannot be negative, but NCP/GPP is 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. 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 (Fig. 5) as described by the fitted regression equation:

$$\log \mathrm{GPP/CR} = -0.43 + 0.74\,(\pm 0.06)\,\log \mathrm{GPP}$$

$$(R^2 = 0.48,\ p < 0.0001,\ N = 158)$$

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

$$\mathrm{NCP} = -3.29 + 0.92\,(\pm 0.03)\,\mathrm{GPP}\ (R^2 = 0.86,\ p < 0.0001,\ N = 165)$$

There was also positive relationship between GPP and chlorophyll *a* for the stations and cruises where the data were available (Fig. 6).

Depth-integrated metabolic rates, integrated down to 20 m, were calculated for each station (Table 3). Integrated NCP ranged broadly from −251.6 to

1065.5 mmol O_2 m^{-2} d^{-1}. The lowest value was measured in the central Fram Strait during summer 2007, whereas the higher was measured in the Kongsfjorden during spring 2011 (Table 3). The minimum integrated GPP was 0 mmol O_2 m^{-2} d^{-1} during the late fall-early winter cruise, conducted under 24 h of darkness, and the maximum integrated GPP was 1073.1 mmol O_2 m^{-2} d^{-1} measured in the Kongsfjorden during the spring cruise in 2011 (Table 3). The minimum integrated CR rate (0.35 mmol O_2 m^{-2} d^{-1}) was measured in the Barents Sea during the late fall-early winter cruise and the maximum (475.8 mmol O_2 m^{-2} d^{-1}) in the central Fram Strait during summer 2007 (Table 3).

In late fall–early winter cruise, in absence of light, all stations supported net heterotrophic communities. In spring, at the onset of the 24 h daylight period, communities are expected to be strongly autotrophic. Indeed, all stations had net autotrophic communities in early spring 2007, but the community at one of the three stations sampled in 2008 was net heterotrophic. The extreme low temperature and heavy ice cover encountered during early spring did not yield the appropriate conditions for bloom development. In May all stations were net autotrophic and the GPP/CR ratio was very high, with great production and low respiration rates, indicative of a bloom development. In the late spring–early summer cruise conducted in 2009 one of the eight sampled stations were found to be net heterotrophic. In the summer cruises a total of 40 % ($N = 22$) and 33 % ($N = 7$) of the stations were found to support net heterotrophic communities in 2007 and 2008, respectively.

4 Discussion

4.1 Methods used

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

Alternative methods to estimate planktonic metabolism, avoiding "bottle effects" include the assessment of the biological O_2 saturation, which refers to the differences between O_2 and Ar saturation (Quay et al., 1993), and the triple oxygen isotope composition (^{16}O, ^{17}O, and ^{18}O) of dissolved O_2 (Luz and Barkan, 2000). The method of triple oxygen isotopes composition estimates gross production integrated on spatial and temporal scales from the differences between the oxygen triple isotope composition (^{16}O, ^{17}O and ^{18}O) of atmospheric and dissolved O_2 and the rate of air-sea oxygen exchange (Luz and Barkan, 2000). In addition to this method, O_2/Ar gas ratios measured in situ can be combined with the oxygen triple isotope composition to estimate rates of NCP (Bender, 2000; Hendricks et al., 2004). The combination of these methods to estimate community metabolism remove the "bottle effect" and integrate metabolic rates over period of weeks to months, but has a high associated error, from 30 to 40 % (Juranek and Quay, 2005; Robinson and Williams, 2005).

Estimation of NCP in the upper water column can also be made from direct analysis of decreases in total dissolved inorganic carbon (DIC) after correcting for CO_2 exchange with the atmosphere. However, before the mid 1980s, when a coulometric technique for total DIC analysis was developed (Johnson et al., 1985, 1987), measurements

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of total DIC concentration in seawater were not accurate enough to determine NCP (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 4) 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 4), 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.

The 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, 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 3), the respiratory carbon demand to be $75.26 \pm 30.46\,\mu\text{mol}\,\text{l}^{-1}$ during the dark period. This is below the average DOC pool in the area studied ($89.01 \pm 2.46\,\mu\text{mol}\,\text{C}\,\text{l}^{-1}$, Table 2), suggesting that the large DOC pool in Arctic waters suffices to maintain significant respiration rates in the plankton community across 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 3). The highest NCP and GPP are both reached in spring (in a bloom stage), when water temperatures remain low and ice cover is reduced (Table 3), with an extremely high GPP/CR ratio, indicative of a spring bloom development, when production increases sharply and respiration rates remain low. In a previous study, (Cottrell et al., 2006) also reported higher metabolic rates in spring than in summer, but their production values were lower than the values reported here (Table 4). These differences can be attributed to differences in the stage of the bloom when the spring sampling was made. Whereas our spring samples were taken in bloom situation (in May), the Cottrell et al. (2006) samples where probably taken during a post-bloom situation, as their GPP/CR ratios are lower than those measured here. The spring bloom in Arctic water can account for a 40 % of the total annual primary production (Lavoie et al., 2009). In addition, our study was conducted mainly in the Fram Strait, whereas their study was conducted in the Chukchi Sea, at lower latitude than our study area, which may affects seasonal development.

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

The GPP/CR ratio increased with increasing GPP, as observed elsewhere in the ocean (see Duarte and Agusti, 1998; Duarte and Regaudie-de-Gioux, 2009), implying that unproductive Arctic communities tend to have a low GPP/CR, thus tending to be heterotrophic. The fitted regression equation implies that the average GPP required to balance Arctic planktonic metabolism is 3.84 mmol O_2 m^{-3} d^{-1}. Use of the relationship between NCP and GPP to derive the GPP required to metabolic balance (i.e. GPP at

NCP = 0) was comparable, at 3.58 mmol O_2 m^{-3} d^{-1}. This rate is 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.

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

An approximation to the annual metabolic rates in the western European Arctic sector can be attempted with the integrated metabolic rates presented here. However, this exercise must be considered a tentative one, due to the sparse sample density over time, particularly during wintertime and transition periods between polar night and midnight sun. The mean annual GPP was calculated to be 32 mol O_2 m^{-2} yr^{-1} (305 g C m^{-2} yr^{-1}) and the mean annual CR was estimated at 20 mol O_2 m^{-2} yr^{-1} (197 g C m^{-2} yr^{-1}), lower than the GPP estimate. Accordingly, these calculations indicate that the mean annual NCP (NCP = GPP – CR) across the study area is expected to be positive at 11 mol O_2 m^{-2} yr^{-1} (108 g C m^{-2} yr^{-1}), implying that the planktonic community in the European sector of the Arctic is likely to be net autotrophic at the annual scale, thereby acting as a significant atmospheric carbon sink. The spring bloom, with a duration of 14 days contributed to the 26 % of the total annual gross primary production. The GPP estimate reported here is a 69 % higher than previous estimates of annual production for this area (average of 93 ± 18 g C m^{-2} yr^{-1}, Wassmann et al., 2006a). The annual NCP value derived here is slightly lower than NPP values derived from satellite-data for the Bering Sea (124 g C m^{-2} yr^{-1}), and bellow the global mean of 140 g C m^{-2} yr^{-1} (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 averaging 23.2 % of the ^{14}C primary production (Alcaraz et al., 2010).

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).

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 °C 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 may even decrease in the future. Warming can result in weaken substantially the role of Arctic communities as significant CO_2 sinks and may even be reverted to become CO_2 sources to the atmosphere (Vaquer-Sunyer and Duarte, 2010) because warming is predicted to increase the carbon flow through bacteria and that most of the carbon consumed would be released as CO_2 (Kritzberg et al., 2010). Rising temperature also affects ice melting, thereby also affecting the production of ice algae, and increases river discharge (Peterson et al., 2002), which may lead to higher DOC inputs to the Arctic Ocean (Cooper et al., 2005), possibly supporting higher pelagic respiration rates. Global warming results in an “atlantification” of large regions in the Atlantic sector of the Arctic Ocean (Wassmann et al., 2004). Implications of “atlantification” will be multiple, affecting vertical mixing and introducing Atlantic species that competitively displace Arctic species poleward, among others. However, the effects of “atlantification” of the Arctic metabolic rates are unknown. As atlantification is expected to reduce stratification, it will result in significant changes in phytoplankton composition, bloom size and development, and vertical flux possibly leading to a regime shift in the Arctic marine ecosystem (Wassmann et al., 2004).

Ice melting can also produce a decrease in primary production (Regaudie-De-Gioux and Duarte, 2010; Duarte et al., 2012), consistent with the positive relationship between chlorophyll *a* and salinity reported here. These results are in contrast with earlier findings for the Southern Ocean that suggest that freshwater discharge with ice melting should increase primary production due to increased stratification (Montes-Hugo et al., 2009; Montes-Hugo et al., 2010).

The results presented here provide a first assessment of seasonal and spatial variability in planktonic metabolism in the Western European sector of the Arctic, allowing the evaluation of patterns in metabolic rates and a first, albeit rough, approximation of the annual metabolic balance of Arctic plankton communities. The estimates derived here can be improved further 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, b). 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.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/9/7701/2012/ bgd-9-7701-2012-supplement.pdf.

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Table 1. Summary of water temperature (°C), Salinity (psu) and chlorophyll *a* content average (± SE) and range, and the corresponding ice conditions for the different cruises and different sampled areas (and number of stations sampled at each area) for the depths where metabolism was assessed.

Cruise	Dates	Study area (number of stations)	Number of stations	Water temperature (°C)	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	17/06/2009–25/07/2009	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) Isfjord (2) Kongsfjorden (1) Van Mijenfjord (1) North Spitsbergen (2)	12	0.35 ± 0.27 (−1.6 to 4.1)	34.4 ± 0.1 (33.7 to 35.1)	nd	Open waters – ice presence

nd: no data

Table 2. Dissolved organic carbon (DOC, μmol C l^{-1}) data reported in literature and this study for the studied area at the studied period.

	DOC (μmol C l^{-1})				
Study	Mean	SE	Maximum	Minimum	*N*
Tovar-Sánchez et al. (2010)	93.95	4.50	123.66	79.26	9
Kritzberg et al. (2010)	104	25.7	181	78	4
This study	89.01	2.46	132.65	65.11	42

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

volumetric		ARCTOS Fall/Winter 06	IAOOS 07 Spring 07	ATOS Summer 07	IAOOS 08 Spring 08	JM 08 Summer 08	ATP 09 Spring 09	ATP 10 Spring 10	ATP 11 Spring 11
NCP	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
	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
CR	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
	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
GPP	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
	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
GPP/CR	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
	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
NCP/GPP	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
	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									
NCP	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
	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
CR	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
	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
GPP	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
	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
GPP/CR	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
	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
NCP/GPP	Mean		0.58	−0.04	−0.19	−0.07	0.65	1.06	0.74
	SE			0.21		0.17	0.11	0.22	0.17
	Minimum			−1.78		−0.9	0.24	0.66	−0.08
	Maximum			0.84		0.22	0.89	2.12	1.47
	N		1	14	1	6	5	6	8

Table 4. Average planktonic metabolic rates ($mmol\,O_2\,m^{-3}\,d^{-1}$) for different studies of planktonic community metabolism in the Arctic Ocean. Rates given as gross primary production (GPP), net community production (NCP) and respiration (*R*). Number of measurements included for each rate is given (*N*).

Authors	Region	Date	Season	GPP	NCP	CR
Cota et al. 1996[*]	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 et al. (2006)[*]	Chukchi Sea	07/94–07/96	All	5.74 (50)	2.25 (110)	3.01 (59)
Cottrell et al. (2006)[*]	Chukchi Sea	07–08/2002 and 07–08/2004	Summer	5.41 (43)	1.90 (93)	2.51 (50)
Cottrell et al. (2006)[*]	Chukchi Sea	05/2004	Spring	7.76 (7)	4.14 (17)	5.80 (9)
Cottrell et al. (2006)[*]	Chukchi Sea	16/07/2002–26/08/2002	Summer	4.30 (29)	1.90 (54)	1.12 (35)
Cottrell et al. (2006)[*]	Chukchi Sea	16/07/2004–26/08/2004	Summer	7.71 (14)	1.90 (39)	5.75 (15)
Hameedi (1978)[*]	Chukchi Sea	07/1974	Summer	9.45 (42)		
Apollonio (1980)	Dumbell Bay	09/07/1959–09/07/1959	Summer	3.17 (11)	3.92 (11)	
Harrison et al. (1982)	Baffin Bay	26/08/1978–21/09/1978	Summer	0.77 (14)		
Olli et al. (2007)[*]	Central Arctic	26/07/2001–18/08/2001	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)

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

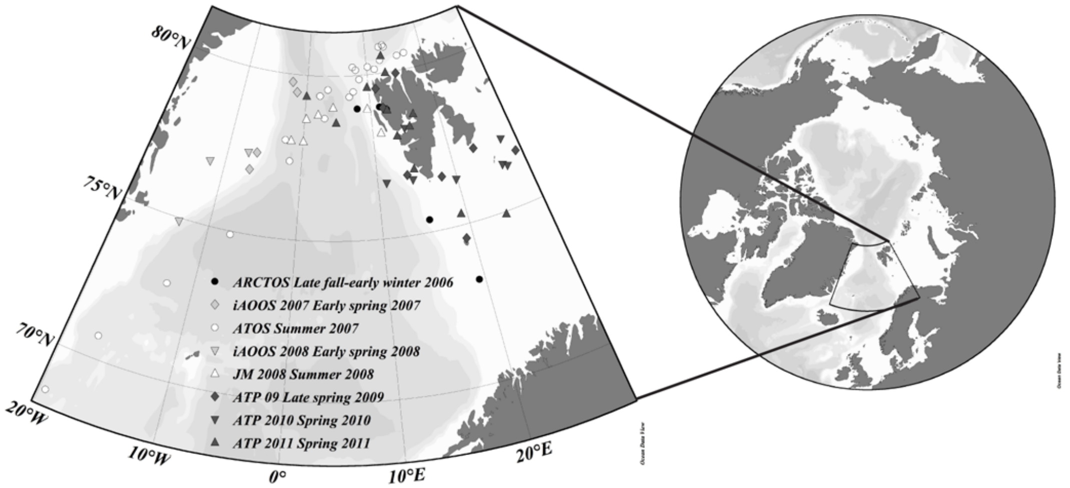

Fig. 1. Map showing the location of the stations sampled along the 5 cruises covering the northern Fram Strait, Spitsbergen waters and the western Barents Sea.

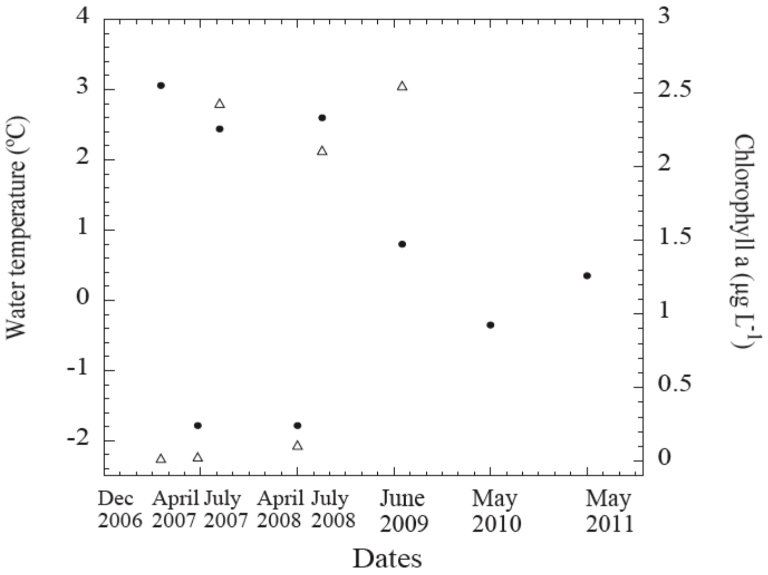

Fig. 2. Mean (± SE) surface seawater temperature (°C, circles) and chlorophyll *a* (µg Chl *a* l^{-1}) concentration (triangles) over time.

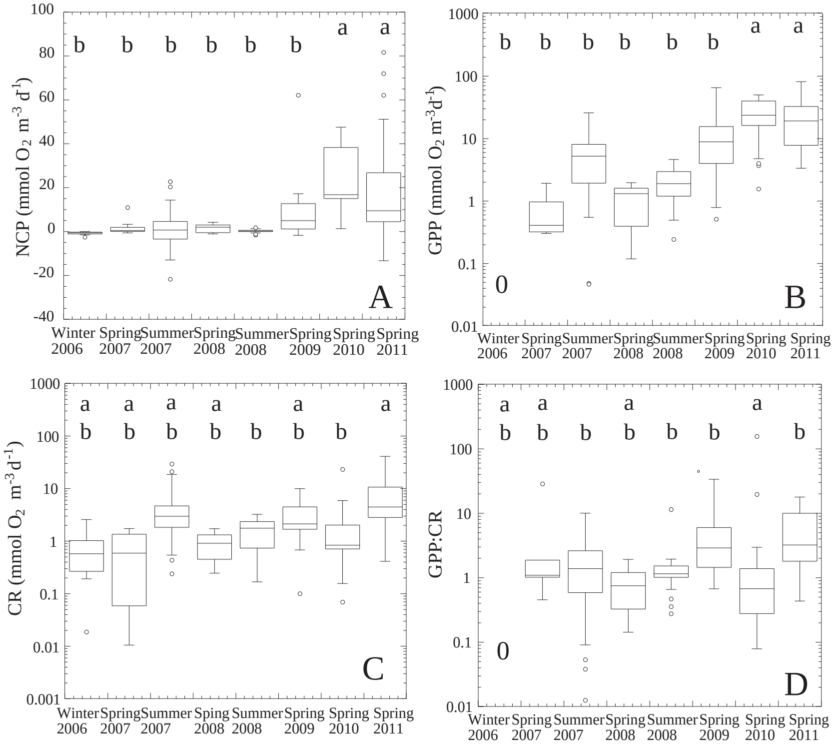

Fig. 3. Box plots showing the distribution of metabolic rates for the different cruises presented here: **(A)** Net Community Production (NCP), **(B)** Community Respiration Rate (CR), **(C)** Gross Primary Production (GPP) and **(D)** the ratio of GPP to CR. All rates reported in mmol O_2 m^{-3} d^{-1}.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

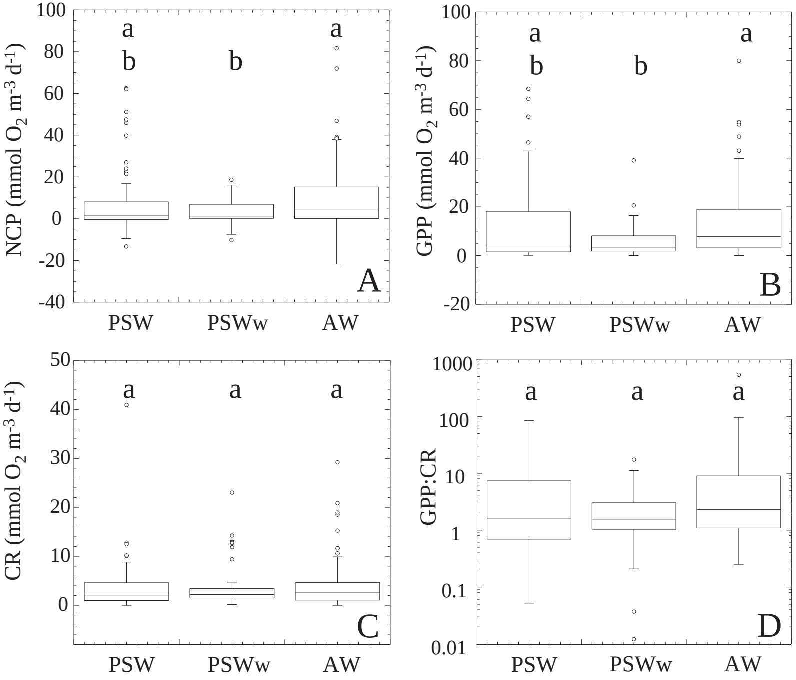

Fig. 4. Box plots showing the distribution of metabolic rates for the different water masses sampled here: **(A)** Net Community Production (NCP), **(B)** Community Respiration Rate (CR), **(C)** Gross Primary Production (GPP) and **(D)** the ratio of GPP to CR. All rates reported in mmol O_2 m^{-3} d^{-1}. The boxes show the median of the metabolic rates plus the lower (25 %) and upper (75 %) quartiles, the whiskers indicate 1.5 times the Interquartile Range (IQR). Letters indicate the results for a Tukey HSD-test, whereby the metabolic rate did not differ significantly for cruises with the same letter.

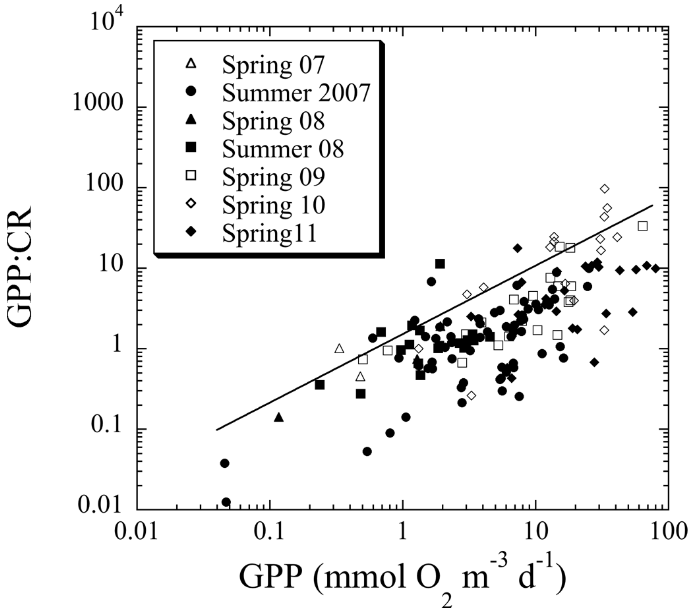

Fig. 5. The relationship between the ratio of gross primary production to community respiration (GPP/R) and gross primary production (mmol O_2 m^{-3} d^{-1}) in the different cruises. The solid line shows the fitted regression equation.

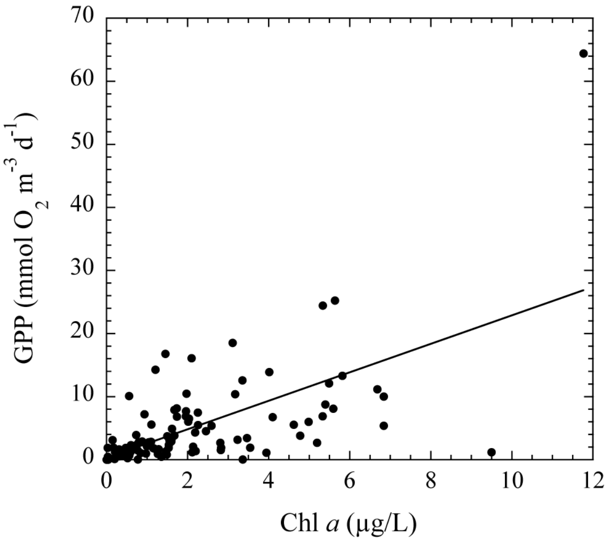

Fig. 6. The relationship between Gross Primary Production (GPP) and chlorophyll *a* concentration. The solid line shows the fitted regression equation GPP (mmol O_2 m^{-3} d^{-1}) = 0.30 + 2.26 (±0.29) Chl *a* (µg Chl *a* l^{-1}) (R^2 = 0.38, $p < 0.0001$, N = 98).