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Plankton metabolism and bacterial growth efficiency in offshore waters along a latitudinal transect between the UK and Svalbard

E.E. García-Martín [a,*], S. McNeill [b], P. Serret [a], R.J.G. Leakey [b]

[a] Dept. Ecología y biología animal, Facultad de Ciencias del Mar, Universidad de Vigo, CP 36210 Vigo (Pontevedra), Spain
[b] Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll, PA37 1QA Scotland, UK

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ABSTRACT

Euphotic zone gross primary production, community respiration and net community production were determined from *in vitro* changes of dissolved oxygen, and from *in vivo* INT reduction capacity fractionated into two size classes, in offshore waters along a latitudinal transect crossing the North, Norwegian and Greenland Seas between the UK and Svalbard. Rates of gross primary production were higher and more variable than community respiration, so net autotrophy prevailed in the euphotic zone with an average net community production of 164 ± 64 mmol O_2 m^{-2} d^{-1}. Respiration seemed to be mainly attributed to large eukaryotic cells (> 0.8 μm) with smaller cells, mainly bacteria, accounting for a mean of 25% (range 5–48%) of community respiration. Estimates of bacterial growth efficiency were very variable (range 7–69%) due to uncoupling between bacterial respiration and production. Larger cells tended to contribute more towards total respiration in communities with high gross primary production and low community respiration, while bacteria contributed more towards total respiration in communities with lower gross primary production, typical of microbial-dominated systems. This suggests that community respiration is related to the size structure of the plankton community.

1. Introduction

Understanding the biotic mechanisms that mediate the marine carbon cycle is a major research objective in biological oceanography. The main biological processes involved are gross primary production (GPP), community respiration (CR), and the loss of biogenic carbon to sediments (Rivkin and Legendre, 2001). In steady state conditions, the difference between GPP and CR (*i.e.* the net community production, NCP) represents the net contribution of the marine biota to carbon export and hence plays a key role in the regulation of ocean CO_2 concentration, air–sea exchange and climate. However steady-state conditions are seldom, if ever, realised in the ocean and this, along with the complex dynamics of planktonic ecosystems, renders elucidation of the role of marine biota in the marine carbon cycle challenging.

Planktonic primary production is known to be limited by light, temperature and nutrients (Field et al., 1998), while temperature and organic matter availability are the main factors that constrain CR (Sampou and Kemp, 1994). In addition, community structure and dynamics influence trophic connections and the fate of organic matter produced (del Giorgio and Williams, 2005; Pace and Cole, 2000). Knowledge of the processes controlling the magnitude and variability of primary production is sufficient to delineate marine biogeographic provinces (Longhurst, 1998) and to remotely estimate water column primary production from the optical properties of surface waters (Behrenfeld and Falkowski, 1997; Pabi et al., 2008). By contrast, the processes controlling the variability of CR are still poorly understood. The evaluation of the net metabolic balance (*i.e.* NCP) offers an integrative approach to examine the biological contribution to the carbon cycle, encompassing individual autotrophic and heterotrophic processes and the dynamics emerging from their interactions; however, GPP and CR do not respond to environmental factors in a uniform or consistent manner, complicating short-term predictions of NCP. For example, Regaudie-de-Gioux and Duarte (2012) report that the effect of temperature on primary production and respiration depends on the season of the year and region of study across a wide range of ecosystems. Similar observations have been reported by Pomeroy and Wiebe (2001) when studying the effect of temperature and organic material on bacterial activity, while Serret et al. (2009) have found NCP to be dependent on trophic structure and energy flux dynamics.

A positive net metabolic balance implies that a surplus of primary production could be consumed by higher trophic levels of the food web, laterally transported to other communities, or exported vertically to the deep ocean. It is known that the rate of export to deep waters is influenced by the size structure of the

* Corresponding author. Present address: School of Environmental Science, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK. Tel.: +44 1603 593162.
E-mail address: Enma.Garcia-Martin@uea.ac.uk (E.E. García-Martín).

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planktonic community: a community composed of small cells are expected to have a lower rate of sedimentation compared to a community composed of larger organisms where grazing is less tightly coupled and sinking rates are higher (Kiørboe, 1993; Legendre and Rassoulzadegan, 1995). Moreover, communities dominated by small organisms and complex food webs are expected to respire a larger proportion of autotrophic production within the euphotic zone leaving less organic matter available for export (Michaels and Silver, 1988). Indeed, low rates of primary production are often associated with plankton communities dominated by small-sized cells (Kiørboe, 1993; Legendre and Le Fevre, 1991) with a high contribution of heterotrophic microorganisms to CR and resulting low or negative NCP. During the last two decades considerable attention has been paid to the relationship between primary production and phytoplankton size (Legendre and Le Fevre, 1991), the trophic structure of the food web (Kiørboe, 1993; Serret et al., 2001; Smith and Kemp, 2003) and the export rate (Legendre and Rassoulzadegan, 1995; Tremblay and Legendre, 1994; Wassmann, 1990); however, the contributions of different components of the plankton community to CR and NCP are still poorly understood.

Measurements of CR and, especially, bacterial respiration (BR) are rare compared to the data available on primary production. Bacteria are considered to be major contributors to total CR (del Giorgio et al., 2011; Lemée et al., 2002; Rivkin and Legendre, 2001) remineralising the bulk of organic matter within the water column and thereby exerting a major influence on carbon and nutrient cycles. BR has usually been estimated from changes in the dissolved oxygen concentration in a pre-filtered sample after *in vitro* incubations (Reinthaler and Herndl, 2005; Robinson et al., 2002b), or derived indirectly from CR (Robinson and Williams, 2005) or bacterial production (BP) measurements (del Giorgio and Cole, 2000; del Giorgio and Cole, 1998). The latter approach has the disadvantage of assuming a constant relationship of BR to BP or CR, while the former has been criticised due to filtration and incubation effects. The physical separation of cells of different size by filtration alters both the community structure (Gasol and Morán, 1999) and the activities of each size class (Aranguren-Gassis et al., 2012). Long incubations times, as required for BR measurements (at least 24 h in non-cultured samples), lead to further bias. BR estimates based on short incubation times, or an improved evaluation of the relationship between BR and CR/BP, are therefore required across different regions to improve the characterisation of the carbon flow through bacteria and its impact on food web dynamics, net metabolic balance and the carbon cycle. Furthermore, it is important to attain BR and BP measured concurrently at the same temporal and spatial scale in order to calculate bacterial growth efficiency (BGE = BP/(BP + BR)) which, in turn, determines the relationship between bacterial carbon demand and bacterial biomass produced (del Giorgio and Cole, 1998).

Recently the *in vivo* reduction of the 2-(*ρ*-iodophenyl)-3-(*ρ*-nitrophenyl)-5phenyl tetrazolium salt (INT) has been employed as a proxy for estimating respiration (Martínez-García et al., 2009). This approach enables estimation of BR during short (<5 h) incubations without pre-filtration, thus avoiding problems associated with long incubation times and the community disruption; however, it has received substantial criticism based on the claim that the method is not specific to enzymes associated with the electron transport system and therefore does not derive an accurate measure of respiration (Maldonado et al., 2012). Despite this criticism, comparisons made between *in vivo* INT reduction capacity and the standard approach of measuring *in vitro* changes in dissolved oxygen in incubated samples, based on data from different oceanographic areas and trophic conditions, reveal that the technique has value as a proxy for estimating respiration (García-Martín et al., *in prep*). Further studies are therefore required in order to establish the validity of INT reduction capacity as a proxy of respiration.

Comparative studies along latitudinal transects are well suited to the study of plankton dynamics in open, non-steady state ocean systems where rapid changes in communities indicate that transient non-equilibrium situations are frequent at small temporal and spatial scales. Such studies allow correlation of biogeochemical and ecological variables in planktonic ecosystems, evaluating general trends, functions and relationships as a function of contrasting biotic and abiotic factors (Robinson et al., 2006). However, it is difficult to discern causality from such studies, especially when the focus is on complex community dynamics due to the interactions with, and feedbacks from, community structure and function. Most studies of plankton metabolism conducted using latitudinal transects have been performed across temperate and/or tropical waters (Morán et al., 2004; Robinson et al., 2002a; Serret et al., 2002) with few undertaken across temperate and Arctic waters (Gosselin et al., 1997; Luchetta et al., 2000; Rey et al., 2000).

The aim of the present study was to characterise microbial plankton metabolism and associated physicochemical variables in offshore waters along a latitudinal transect between the UK and Svalbard, crossing three marine biogeochemical provinces. In particular (i) GPP, CR and NCP were determined from *in vitro* changes in dissolved oxygen concentration in the euphotic zone, contributing to the meagre database of CR and NCP values available from high latitude waters; (ii) BR was determined in non-fractionated samples, for the first time in these waters, via the *in vivo* INT reduction capacity of plankton cells during short incubations (2–4 h); and (iii) BGE was determined from estimations of BR and BP conducted concurrently over similar time scales, thereby reducing the potential bias associated with the conventional approach of combining BR and BP measurements undertaken using differential incubation times.

2. Materials and methods

2.1. Study site

The study was undertaken between the 14 and 19 June 2010 as part of the UK ICECHASER II research cruise on the RSS *James Clark Ross* (cruise JR219). Six stations were sampled in offshore waters along a latitudinal transect from the UK to the Svalbard archipelago crossing the North, Norwegian and Greenland Seas (Fig. 1 and Table 1). The transect encompassed three oceanographic provinces, as defined by Longhurst (1998): (i) the Northeast Atlantic Shelves province (NECS) which included the Central North Sea (CNS) and Northern North Sea (NNS) stations; (ii) the Atlantic Subarctic province (SARC) which included the Southern Norwegian Sea (SNWS), Central Norwegian Sea (CNWS) and Northern Norwegian Sea (NNWS) stations; and (iii) the Atlantic Arctic Province (ARCT) which included the Eastern Greenland Sea (EGS) station.

2.2. Physical and chemical variables

Shipboard temperature, salinity and fluorescence measurements were undertaken at each station using Sea-Bird Electronics SBE 911 and SBE 917 series CTD profilers and a Chelsea Aqua 3 fluorometer. The salinity sensors were calibrated during the cruise. Fluorescence values were converted to units of chlorophyll using a depth-dependent conversion factor derived from chlorophyll measurements undertaken on water samples collected during the cruise (T. Jackson personal communication). To determine inorganic nitrate + nitrite, ammonium, silicate and phosphate concentrations, water samples ($\sim$40 ml) were collected using 10 l

Niskin sampling bottles from up to 8 depths up to 200 m at each station. Each sample was screened through a 25 mm diameter glass fibre (GF/F) filter and triplicate aliquots analysed on ship by colorimetric flow injection analysis using a Lachat *QuikChem 8500* flow injection autoanalyser following the manufacturers recommended methods. These methods are adaptations from standard seawater analyses given by Grasshoff et al. (1999).

2.3. Biological analyses

Water samples (~8 l) were collected early morning at each station using 10 l Niskin sampling bottles from up to 4 depths in the euphotic zone (as defined by the depth of 1% incident irradiance): (i) the surface (2–5 m), (ii) the chlorophyll maximum, (iii) the depth of 1% irradiance, and (iv) an intermediate depth between the surface and 1% irradiance. The sea water was then carefully transferred to 10 l carboys, using a silicone tube, for subsequent subsampling and analysis of GPP, CR NCP and BR, as outlined below. For BP, water samples (~50 ml) were collected from 5 depths in the upper 41 m including the euphotic zone depths.

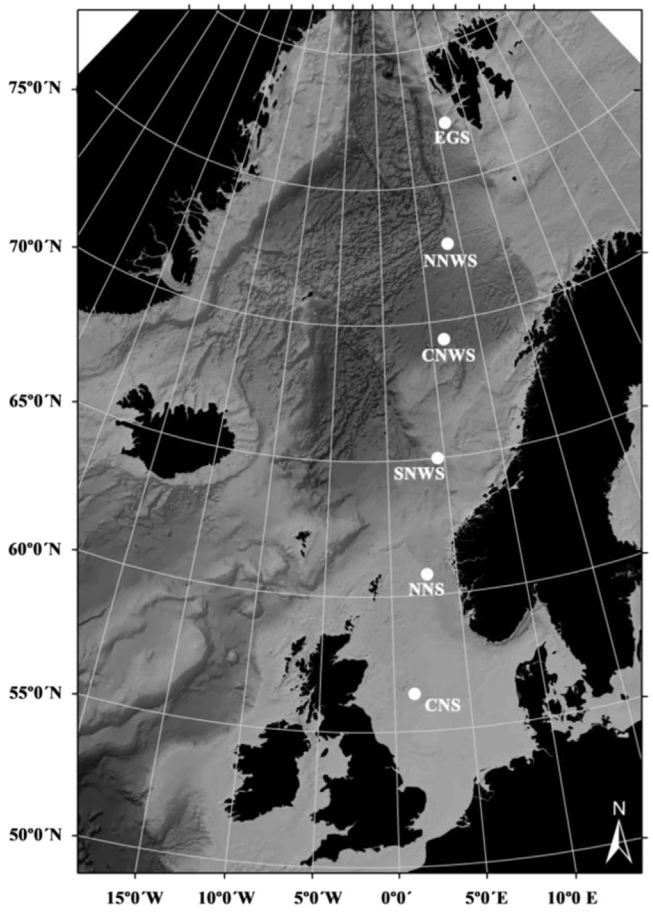

Fig. 1. Map of the stations sampled between the UK and Svalbard.

2.3.1. *In vitro gross primary production, community respiration and net community production by oxygen concentration*

GPP, CR (referred to hereafter as CR_{O_2} to distinguish it from CR estimated by the *in vivo* INT reduction capacity assay – see Section 2.3.2) and NCP were measured by monitoring changes in oxygen concentrations after 24 h light-dark bottle incubations. Dissolved oxygen concentration was measured by automated precision Winkler titration performed with a Metrohm 721 DMS Titrino titrator, utilising a potentiometric end point as described in Serret et al. (1999). Eight gravimetrically calibrated 125 ml opaque "dark" borosilicate glass bottles and four transparent "light" bottles were carefully filled with water from each depth. Water was allowed to overflow during the filling, and special care was taken to prevent air bubble formation in the silicone tube. For each depth, four replicate dark bottles were fixed immediately for the measurement of initial oxygen concentrations (t_{zero}). The four light and remaining four dark bottles were incubated for 24 h in deck incubators, under natural sunlight with neutral and blue density screening to achieve ambient *in situ* incident irradiance, and fixed for the measurement of final oxygen concentrations (t_{24}). Incubation temperature was maintained with *in situ* water, pumped from 5 m depth, flowing through the incubation system. NCP and CR_{O_2} rates were estimated from the difference in oxygen concentration between the means of the initial (t_{zero}) measurements and the replicate light and dark incubated (t_{24}) samples, respectively (*i.e.* $NCP = [O_2]_{t_{24}(light)} - [O_2]_{t_{zero}}$; $CR_{O_2} = [O_2]_{t_{zero}} - [O_2]_{t_{24}(dark)}$). GPP rates were calculated from $NCP + CR_{O_2}$.

The mean percentage coefficients of variation (% ratio of the s.d. to the mean) of the oxygen concentration in each of the t_{zero}, dark and light analyses were 0.1, 0.1 and 0.2 respectively ($n=23$) and the average of the propagated standard errors (s.e.) of the derived GPP, CR_{O_2} and NCP rates, calculated as $\sqrt{s.e._{t_{zero}}^2 + s.e._{t_{24}}^2}$, were 0.44, 0.27 and 0.41 respectively. The complete data set including individual s.e. of every measurement is shown in Supplementary Table S1, will be deposited at the public global respiration database:

http://www.uea.ac.uk/environmental-sciences/people/People/Faculty+and+Research+Fellow/robinsonc#research (data compiled and maintained by Carol Robinson).

2.3.2. *In vivo community and bacterial respiration by INT reduction capacity assay*

CR and BR (referred to hereafter as CR_{INT} and BR_{INT} to distinguish them from the CR measured by changes in oxygen concentration – Section 2.3.1) were estimated by *in vivo* INT reduction capacity assay (Martínez-García et al., 2009) on samples

Table 1
Dates, acronym, location, CTD rosette number and physicochemical descriptors of stations sampled between the UK and Svalbard.

Sampling date	Station name	Station abbreviation	Latitude	Longitude	CTD No	Descriptors	Longhurts province
14/06/2010	Central North Sea	CNS	56.41 N	1.31 E	2	Stratified, warm water, low nutrient, low chlorophyll, shelf station	NECS
15/06/2010	Northern North Sea	NNS	60.74 N	2.73 E	4	Stratified, warm water, low salinity, low nutrient station	NECS
16/06/2010	Southern Norwegian Sea	SNWS	65.04 N	4.4 E	6	Stratified, low nutrient, open water station	SARC
17/06/2010	Central Norwegian Sea	CNWS	69.34 N	6.37 E	8	Well-mixed, cold water, high nutrient, open water station	SARC
18/06/2010	Northern Norwegian Sea	NNWS	72.75 N	8.27 E	10	Well-mixed, cold water, high nutrient, low chlorophyll, open water station	SARC
19/06/2010	Eastern Greenland Sea	EGS	77.16 N	11.29 E	12	Well-mixed, cold water, shelf station	ARCT

from two depths only (5/6 m and the chlorophyll maximum) at each station. Four 200–250 ml polypropylene opaque plastic bottles were filled with seawater from each 10 l carboy. One replicate was immediately fixed by adding formaldehyde (2% w/v final concentration) and used as a killed control. Fifteen minutes later all four replicates were inoculated with a sterile solution of 7.9 mM iodonitrotetrazolium salt to give a final concentration of 0.8 mM. The solution was freshly prepared for each experiment using Milli-Q water. After 2–4 h incubation under ambient conditions (as outlined in Section 2.3.1), samples were fixed by adding formaldehyde, as for the killed control. Samples were sequentially filtered after 15 min through 0.8 and 0.2 μm pore size polycarbonate filters, air-dried, and stored frozen in 1.5 ml cryovials at −20 °C until further processing. The CR_{INT} (*i.e.* the sum of respiration of the >0.8 μm and 0.2–0.8 μm fractions) and BR_{INT} (considered as the respiration of the 0.2–0.8 μm fraction) were measured following Martínez-García et al. (2009). The respiration of the large size-fraction ($R_{INT} > 0.8$) will result mainly from the activity of eukaryotes and particle attached prokaryotes. By contrast, the main respiring organisms in the small size-fraction (BR_{INT}) will have been heterotrophic bacteria as these comprised from 94% to 99% of the picoplankton abundance as determined by flow cytometry (R. Leakey, personal communication). The use of the INT reduction capacity assay assumes that the tetrazolium salt can penetrate plankton cells easily and at rate independently of cell size and growth state; however, this assumption has not been tested yet and could compromise the BR estimates.

A time-course experiment was conducted during the same research cruise, but subsequent to the current study, on 24 June 2010 on water collected from 5 m depth in colder Arctic waters to determine the optimal incubation time for *in vivo* INT reduction capacity by natural plankton (García-Martín et al., accepted for publication). The optimal incubation time was found to be <5 h and this was adopted as the maximum incubation time for the INT reduction capacity assay.

2.3.3. Bacterial production and bacterial growth efficiency

BP was determined from [^{14}C]leucine incorporation (Kirchman, 2001). For each sample, 20 μl of an aqueous stock solution of L-[U-[^{14}C]leucine (0.306 Ci m mol^{-1}) was added to each of four 3.2 ml sub-samples to give an estimated ~20 nM final concentration, and the contents mixed. Each sub-sample was then incubated in the dark at ambient temperature for either 0, 1, 2 and 3 h after which 160 μl of 20% paraformaldehyde was added. Each sub-sample was filtered onto a 0.2 μm × 25 mm diameter polycarbonate filter and washed with 0.2 μm filtered deionised water. Each filter was then placed in a scintillation vial, dried at room temperature and mixed with 10 ml scintillation fluid (Optiphase HiSafe II). Radioactivity in the sub-samples was measured using a Beckman Coulter LS6500 liquid scintillation counter, with the efficiency of counting determined using the external quench monitor method. [^{14}C]leucine incorporation was calculated from counts (corrected for quenching) according to Kirchman (2001) using isotope specific activity values corrected for decay (Stewart and Hawcroft, 1977). Bacterial population growth (cells m^{-3} d^{-1}) was then calculated from [^{14}C]leucine incorporation using a theoretical approach and assuming no isotope dilution (Kirchman, 2001). Finally, BP (mg C m^{-3} d^{-1}) was calculated from growth using a bacterial carbon conversion factor of 6.3 fg C cell^{-1} (Kawasaki et al., 2011).

Despite their limitations (discussed in Section 4.2), [^{14}C]leucine incorporation and INT reduction capacity assays can be considered to derive good estimates of BP and BR, as demonstrated by their use in previous studies (*e.g.* Ducklow, 2000; Martínez-García et al., 2009; Teira et al., 2013). BGE was therefore calculated from paired BR_{INT} and BP data as: $BGE = BP/(BP + BR_{INT})$, with BR_{INT} converted to carbon units using the linear regression between CR_{O_2} and CR_{INT} assuming a respiratory quotient of 1.

2.4. Data analyses

All GPP, CR_{O_2} and NCP values are presented as mean with standard error (s.e.) unless otherwise stated. Integrated GPP, CR_{O_2}, NCP and BP rates were calculated by trapezoidal integration of volumetric rates measured at the different light depths throughout the euphotic zone. The standard errors of integrated rates were calculated following the propagation procedures for independent measurements described by Miller and Miller (1988). GPP and CR_{O_2} were converted to carbon units using a photosynthesis quotient of 1.2 and a respiratory quotient of 1.

Relationships between the hydrography and metabolic variables (GPP, CR_{O_2}, NCP and BP) were examined by ordinary least-square linear regression analyses using SPSS software. The relationships between GPP and CR_{O_2}, and between CR_{O_2} and CR_{INT}, were examined by reduced major axis regression analysis (model II linear regression). Non-parametric tests were used to examine physio-chemical and plankton metabolism correlations.

3. Results

3.1. Physical and chemical environment

The main hydrographic and nutrient features of the UK to Svalbard transect are shown in Fig. 2. The southernmost station (CNS) showed a strong thermal stratification with a thermocline at ~25 m depth just above the euphotic depth. This thermal gradient was weaker at the Northern North Sea and Southern Norwegian Sea stations (NNS and SNWS) but the stratification of the water column was maintained due to lower salinity water (33.6 ppm) located in the upper ~20 m depth of the second station (NNS). The three most northern stations (CNWS, NNWS and EGS) were characterised by cold and well-mixed waters.

The stratified southern stations (CNS, NNS, SNWS) exhibited very low nutrient concentrations from the surface to the bottom of the euphotic layer (25–35 m depth) with higher values in deeper waters. The nutricline, defined as the area with the maximum nutrient concentration gradient, was located at around 25–35 m depth at these stratified stations concurrent with the thermohaline stratification. In the well-mixed waters further north (stations CNWS and NNWS), a more homogenous nutrient distribution was detected with nitrate+nitrite, phosphate and silicate concentrations higher than at the southern stratified waters. The well-mixed northern shelf station (EGS) exhibited phosphate and silicate minima at ~15 m coincident with the chlorophyll maximum.

All stations except the cold shelf station (EGS) were characterised by low chlorophyll concentrations (<1.5 mg m^{-3}) and a subsurface maximum above the nutricline and near the base of the euphotic layer. At the EGS station chlorophyll maxima were observed from 8 m depth down to the bottom of the euphotic zone. The low nitrate+nitrite concentrations at this station, together with the chlorophyll maxima and high silicate concentrations, suggest the presence of non-diatom bloom or post-bloom conditions.

3.2. Plankton metabolism

Fig. 3 illustrates the variation of plankton community metabolic rates in the euphotic layer. There was a strong relationship between GPP and chlorophyll ($R^2 = 0.51$, $p < 0.001$, $n = 23$) (Table 2). The warm,

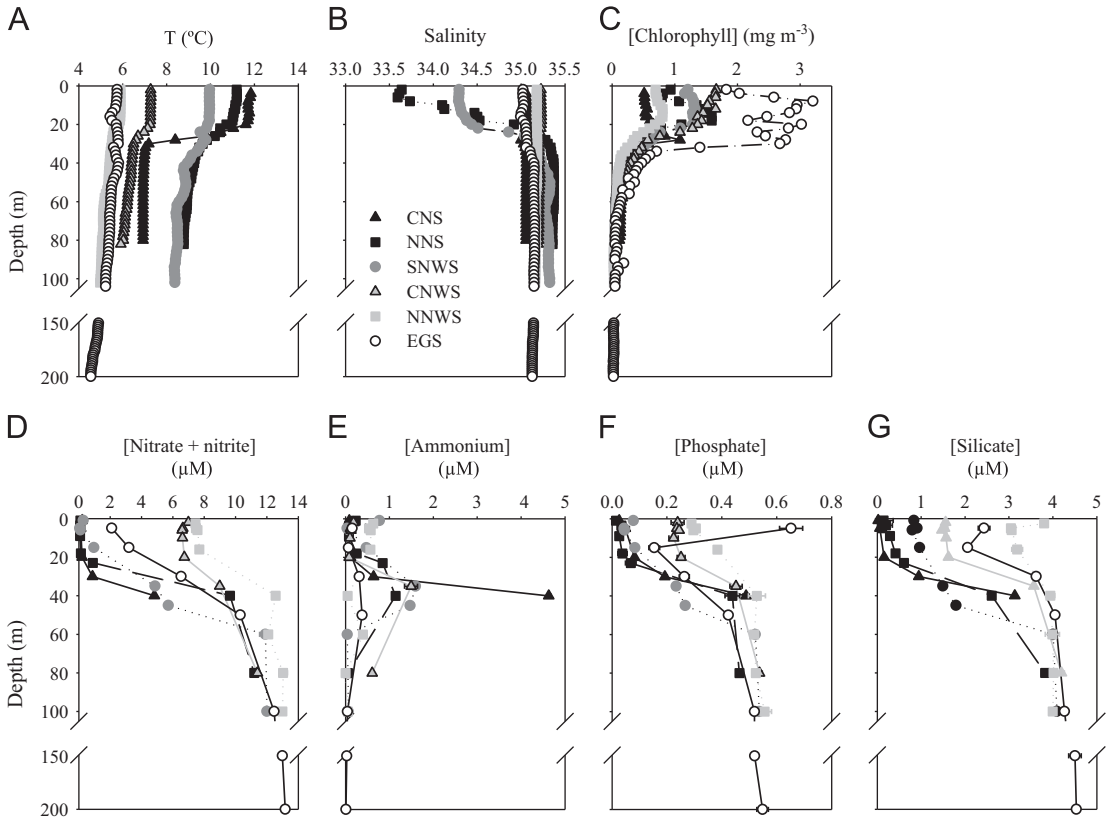

Fig. 2. Vertical profiles of (A) temperature, (B) salinity, (C) chlorophyll, (D) nitrate+nitrite concentration, (E) ammonium concentration, (F) phosphate concentration and (G) silicate concentration at stations between the UK and Svalbard.

stratified shelf station (CNS) exhibited the lowest values of GPP (0.52 ± 0.34–4.29 ± 0.41 mmol O_2 m^{-3} d^{-1}) (Fig. 3A). Intermediate values were observed in the other two warm, stratified stations (NNS and SNWS) and at the cold, well-mixed NNWS station. A subsurface GPP maximum was found at the CNWS station, coincident with the distribution of chlorophyll. By contrast, the cold shelf station (EGS) south of Svalbard exhibited the highest GPP values from the surface down to the base of the euphotic layer (3.54 ± 0.15–23.06 ± 1.14 mmol O_2 m^{-3} d^{-1}), associated with the high chlorophyll maxima and low nitrate+nitrite and phosphate concentrations. These high rates of GPP could be a result of the elevated phytoplankton biomass rather than an increase in activity, as suggested by the lower GPP/chlorophyll ratios (6.4) compared to those observed at the CNWS station (7.4).

Spatial variations in CR_{O_2} were different to those of GPP and not related to chlorophyll (Fig. 3B, Table 2). The warmer, stratified stations together with the cold shelf station (CNS, NNS, SNWS, EGS) exhibited the highest CR_{O_2} rates (> 1.5 mmol O_2 m^{-3} d^{-1}). Respiration at these stations tended to be higher at the surface and decreased throughout the water column to the base of the euphotic layer, except for the warm, shelf station (CNS). Low CR_{O_2} rates ($< 30\%$ GPP) were measured in the cold, well-mixed, open water stations of the Norwegian Sea (CNWS, NNWS).

The wide range of observed GPP values, when compared to CR_{O_2}, suggests that NCP variability was related more closely to GPP rather than to CR_{O_2} (Fig. 3C). Negative NCP values were only measured at the warm shelf station (CNS). The warm open water stations (NNS and SNWS) and the cold well-mixed NNWS station exhibited intermediate NCP values with weak maxima concurrent with the chlorophyll maxima. The moderately high GPP and low CR_{O_2} values observed in the upper 20 m of the CNWS station resulted in high rates of NCP (> 10 mmol O_2 m^{-3} d^{-1}). High NCP values were also recorded from the surface down to the deep chlorophyll maximum at the cold shelf station (EGS) due to relatively high CR_{O_2} values which were balanced by even higher GPP.

Integrated GPP values were, as with volumetric rates, ~4 times more variable than integrated CR_{O_2} (Fig. 4). Integrated GPP values increased from south to north across the stations from 54.2 ± 4.6 mmol O_2 m^{-2} d^{-1} at CNS to 379.1 ± 3.2 mmol O_2 m^{-2} d^{-1} at CNWS, consistent with similar increases in chlorophyll. However, further north at the cold, well-mixed NNWS station, the integrated GPP was lower with values similar to those at the warm, stratified North Sea stations suggesting that the factors controlling GPP were different to those at other stations. Data from this station were therefore not used to explore relationships between integrated variables (Table 3). By contrast, the highest integrated GPP value (481.2 ± 20.2 mmol O_2 m^{-2} d^{-1}) was recorded at the most northerly station (EGS). A strong relationship was observed between integrated GPP, integrated NCP and surface chlorophyll values ($R^2 = 0.99$, $p < 0.001$ and $R^2 = 0.99$, $p < 0.001$, respectively; $n = 5$) (Table 3). However, integrated CR_{O_2} rates did not reflect the general south–north increases of integrated GPP and chlorophyll between stations, with highest values recorded at the two shelf stations (CNS in the south and EGS in the north). Both integrated GPP and NCP varied significantly with temperature and the nutrient availability index (*i.e.* the difference between the nutricline depth and the mixed layer depth), with integrated NCP also significantly related to mixed layer depth; however, CR_{O_2} was not related to any of these variables (Table 3).

CR_{O_2} values were generally lower and less variable than GPP which resulted in a clear uncoupling between these two variables (Fig. 5A) with a GPP:CR_{O_2} ratio > 1 in 91% of the samples. A threshold of net heterotrophy (*i.e.* the value of GPP below which NCP ≤ 0, so GPP $\leq CR_{O_2}$) of 1.5 mmol O_2 m^{-3} d^{-1} was calculated for the entire study using the significant relationship observed between GPP and NCP (Fig. 5B).

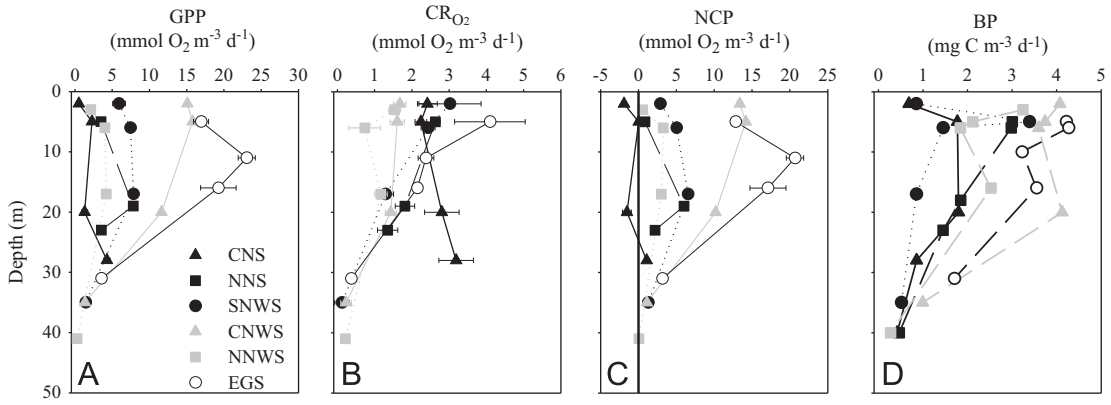

Fig. 3. Vertical profiles of (A) GPP, (B) CR_{O_2}, (C) NCP and (D) BP in the euphotic layer at stations between the UK and Svalbard. Error bars represent the standard error of the measurement.

Table 2
Regression coefficients (R^2) between temperature, salinity, chlorophyll and volumetric metabolic rates measured at stations between the UK and Svalbard. Negative relationships are represented with (−). One asterisk indicates probabilities <0.05, two asterisks <0.01 and three asterisks <0.001. Numbers of data are 23 for GPP, CR_{O_2}, NCP and BP, and 12 for variables derived with the *in vivo* INT reduction assay. Dash denotes no significant relationship.

	T	Salinity	Chl	CR_{O_2}	NCP	BP	CR_{INT}	$R_{INT}>0.8$	BR_{INT}	$\%R_{INT}>0.8$	$\%BR_{INT}$	BGE
GPP	–	–	0.64***	–	0.97***	0.51***	–	–	–	–	–	0.46*
CR_{O_2}	–	–	–	–	–	–	0.42*	0.62**	–	–	–	–
NCP	–	–	0.62***			0.47***	–	–	–	–	–	–
BP	–	–	–				–	–	–	–	–	0.58**
CR_{INT}	–	–	–					–	–	–	–	–
$R_{INT}>0.8$	–	–	–						–	–	–	–
BR_{INT}	–	–	–							–	–	(−) 0.61**
$\%R_{INT}>0.8$	–	–	0.41*									–
$\%BR_{INT}$	–	–	(−) 0.41*									–
BGE	(−) 0.35*	–	0.58*									

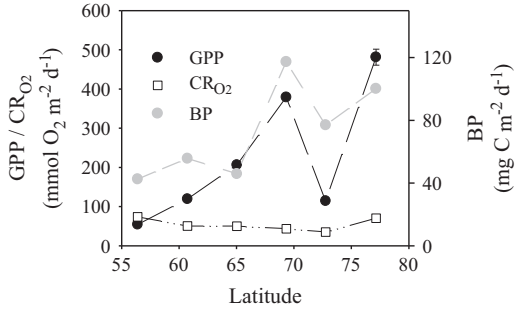

Fig. 4. Latitudinal distributions of euphotic zone integrated GPP (dark symbols), CR_{O_2} (white symbols) and BP (grey symbols) at stations between the UK and Svalbard. Error bars represent the standard error of the measurement.

3.3. Bacterial production

There was a significant relationship between BP and GPP ($R^2=0.51$, $p<0.001$) (Table 2) but no relationship was found between BP and chlorophyll, temperature or CR_{O_2}. BP ranged from ~1% to ~15% of GPP with highest values at surface or subsurface depths, and lowest values at the base of the euphotic layer. The warm stratified stations (CNS, NNS, SNWS) generally exhibited lower BP values compared to the cold mixed stations (CNWS, NNWS, EGS) (Fig. 3D). Integrated BP rates followed a similar trend to GPP, increasing from south to north (Fig. 4) with the cold open-water CNWS station exhibiting the highest integrated BP rate.

3.4. In vivo INT reduction capacity and BGE

A significant relationship was observed between dissolved oxygen consumption and total INT reduction ($CR_{O_2}=18.85(\pm4.77)\times CR_{INT}-0.03(\pm0.03)$, $R^2=0.423$, $p=0.029$, $n=11$) (Fig. 6). Highest CR_{INT} values were recorded in surface (5/6 m depth) waters of the two shelf stations (CNS and EGS), and lowest values in the cold, well-mixed waters of the Norwegian Sea (CNWS, NNWS). These regional differences were mainly caused by the variation of respiration by the large size-fraction community ($R_{INT}>0.8$ μm) which was greater than that of small size-fraction community (BR_{INT}); the latter contributed on average only 24 ± 4% (range 4.5–47.8%) of the total CR_{INT} (Table 4). The contribution of BR_{INT} to CR_{INT} was higher in surface (5/6 m depth) waters than at the chlorophyll maxima, except at the EGS shelf station, where BR_{INT} values were very low compared to $R_{INT}>0.8$ μm at both sample depths. The highest contributions of BR_{INT} to CR_{INT} (≥45%) were recorded in the contrasting surface (5/6 m depth) water environments of the CNS and NNWS stations. A significant relationship was observed between the contribution of the different size fractions ($\%BR_{INT}/CR_{INT}$ and $\%R_{INT}>0.8/CR_{INT}$) and chlorophyll, but not temperature (Table 2).

The absence of relationship between BR_{INT} and BP (Table 2) indicated an uncoupling of bacterial activity which, due to use of similar short-term incubations, cannot be attributed to differing incubation times. A wide range of BGEs, from 6.5% to 68.6% (Table 4), were observed reflecting the high variability of BR_{INT} values. BGE was highest at the SNWS, CNWS stations, and productive EGS station, where the percentage contributions of BR_{INT} to CR_{INT} were generally low. The lowest BGE values were found at the low productivity CNS and NNWS stations, where the % contributions of BR_{INT} to CR_{INT} were highest. BGE was related significantly to BP and BR_{INT} ($R^2=0.58$, $p<0.01$; $R^2=0.61$, $p<0.01$, respectively) (Fig. 7, Table 2), although these relationships could be an artefact of the autocorrelations (BGE is not independent of BP and BR_{INT}, $r=0.61$, $p=0.006$ and $r=-0.78$, $p=0.001$,

Table 3
Regression coefficients (R^2) between physicochemical variables and integrated metabolic rates measured at stations between the UK and Svalbard. Negative relationships are represented with (−). One asterisk indicates probabilities <0.05, two asterisks <0.01 and three asterisks <0.001. Data for the NNWS station are not included. Dash denotes no significant relationship.

	Surface temperature	Surface chlorophyll	Mixed layer depth (MLD)	Nutrient availability index	∫CR_{O_2}	∫NCP	∫BP	*N*
∫GPP	(−) 0.99***	0.99***	–	(−) 0.91*	–	0.99***	0.79*	5
∫CR_{O_2}	–	–	–	–		–	–	5
∫NCP	(−) 0.97**	0.99***	0.81*	(−) 0.86*			0.81*	5
∫BP	–	–	0.85*	–				5

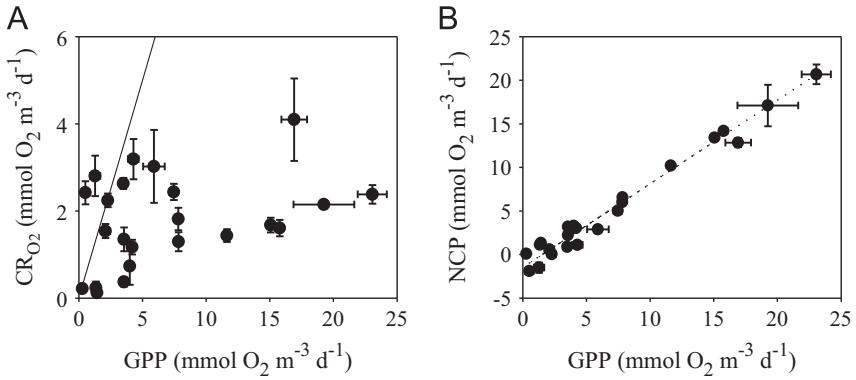

Fig. 5. Relationship between (A) volumetric CR_{O_2} *versus* GPP and (B) volumetric NCP *versus* GPP at stations between the UK and Svalbard. The solid line in (A) represents the 1:1 relationship and the dotted line in (B) the fitted regression linear model II equation: NCP = 0.96(±0.03) GPP − 1.46(±0.31), $R^2=0.98$, $p<0.001$, $n=23$.

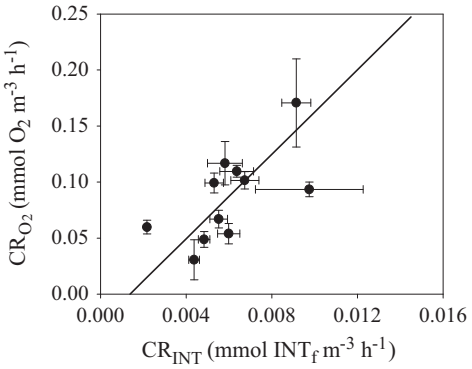

Fig. 6. Relationship between CR_{O_2} *versus* CR_{INT} at stations between the UK and Svalbard. Error bars represent the standard error of the measurement and the solid line indicates the model II regression line: $CR_{O_2} = 18.85(\pm 4.77) \times CR_{INT} - 0.03$ (±0.03); $R^2=0.42$, $p=0.029$, $n=11$.

respectively). Temperature was inversely related to BGE, while chlorophyll and GPP exhibited a positive relationship (Table 2).

4. Discussion

4.1. Variation and control of plankton metabolism

In this study euphotic zone integrated GPP varied between 54.2 ± 4.6 and 481.2 ± 20.2 mmol O_2 m^{-2} d^{-1}. The rates of GPP observed at the most southern stations (CNS, NNS) are within the range of previous values reported in the North Sea (36 ± 11–150 ± 17 mmol O_2 m^{-2} d^{-1}, Robinson et al., 2002b), while rates at the open ocean stations further north were slightly higher values than previous values reported from this region (mean ± s.d. 103.2 ± 72.0 mmol O_2 m^{-2} d^{-1}, Richardson et al., 2005, and 75.2 ± 33.3 mmol O_2 m^{-2} d^{-1} Rey et al., 2000; both calculated assuming a photosynthesis quotient of 1.2).

Temperature is one of the main factors regulating plankton metabolism together with nutrients and light availability (Field et al., 1998; Sakshaug, 2004). Previous studies examining the effect of temperature on plankton production and respiration have shown a clear effect on both variables: increasing temperature enhanced both primary production (Arrigo et al., 2008; López-Urrutia and Morán, 2007) and respiration (Kirchman et al., 2005; Vázquez-Domínguez et al., 2007). However, results derived from this study indicate the opposite response, showing higher GPP at lower temperatures, probably as a consequence of the strong correlation between temperature and nutrients and/or as a result of the longer day length at the colder northern stations. Undoubtedly, temperature is a factor that regulates plankton metabolism (Brown et al., 2004; López-Urrutia et al., 2006; Regaudie-de-Gioux and Duarte, 2012; Yvon-Durocher et al., 2012) although its *in situ* effect could be concealing other factors that correlate with temperature (*e.g.* nutrient availability or water column stability) which could influence not only the individual physiological response but also the structure and function of the community (Kirchman et al., 2005; Marañón et al., 2012; Pomeroy and Wiebe, 2001).

Integrated GPP exhibited a significant positive relationship with surface chlorophyll which might enable the development of a predictive GPP model using surface water optical properties. In addition, the very low variability of CR_{O_2} compared to GPP (see Fig. 4) offers the potential to predict NCP from fluorescence estimates. However, the spatial and temporal variability of this region is very poorly represented by data from one single transect. More data are therefore needed to verify these relationships.

In contrast to GPP, integrated CR_{O_2} did not co-vary with temperature or chlorophyll. The average CR_{O_2} rate across the stations was 53.8 ± 6.2 mmol O_2 m^{-2} d^{-1}, lower than rates measured in summer in the North Sea (131 ± 12.8 mmol O_2 m^{-2} d^{-1}) by Robinson et al. (2002b) but in agreement with those rates measured in summer in the Greenland Sea (53 ± 6 mmol O_2 m^{-2} d^{-1}) by Regaudie-de-Gioux and Duarte (2010).

The higher values of GPP, as compared to CR_{O_2}, resulted in positive NCP values (range −1.9 ± 0.27 to 20.68 ± 1.13 mmol

Table 4
$R_{INT} > 0.8$, BR_{INT}, the contribution of $R_{INT} > 0.8$ and BR_{INT} to CR_{INT}, and BGE from 5/6 m depth (surface) and the deep chlorophyll maximum (DCM) at stations between the UK and Svalbard. Blank data indicate no data available.

Station	$R_{INT} > 0.8$ μM INT_f d^{-1}		BR_{INT} μM INT_f d^{-1}		$R_{INT} > 0.8/CR_{INT}$ %		BR_{INT}/CR_{INT} %		BGE %	
	Surface	DCM	Surface	DCM	Surface	DCM	Surface	DCM	Surface	DCM
CNS	0.12	0.11	0.11	0.03	52.2	78.6	47.8	21.4	6.5	19.1
NNS	0.11		0.04	0.09	73.3		26.7		25.8	6.7
SNWS	0.14	0.13	0.03	0.01	82.4	92.9	17.6	7.1	36.9	32.3
CNWS	0.09	0.04	0.04	0.01	69.2	80.0	30.8	20.0	28.9	57.7
NNWS	0.06	0.09	0.05	0.03	54.5	75.0	45.5	25.0	16.7	29.4
EGS	0.21	0.11	0.01	0.02	95.5	84.6	4.5	15.4	68.6	42.1

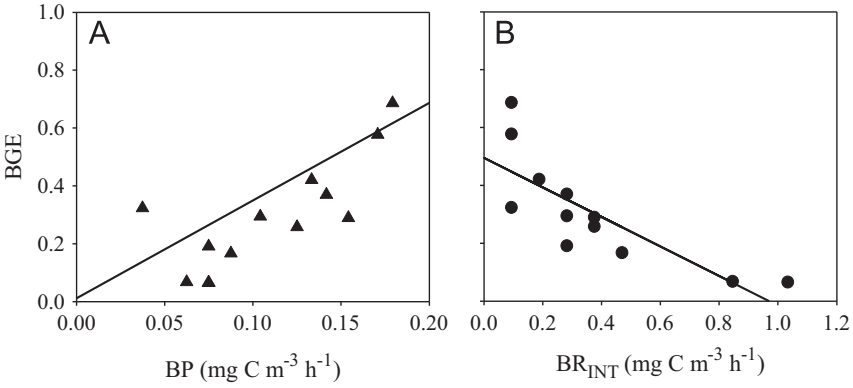

Fig. 7. Relationship between BGE *versus* (A) BP ($R^2=0.58$, $p=0.004$, $n=12$) and (B) BR_{INT} ($R^2=0.61$, $p=0.003$, $n=12$) at stations between the UK and Svalbard. Lines represent the significant relationships.

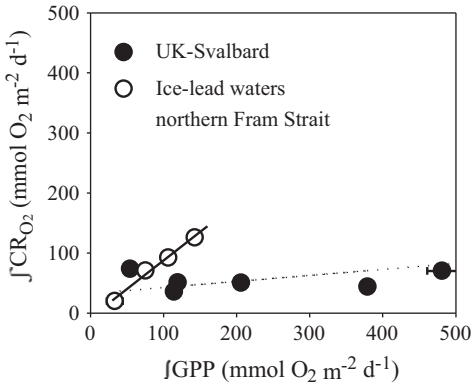

Fig. 8. Integrated CR_{O_2} *versus* GPP at stations between the UK and Svalbard (dark symbols) and at the Arctic ice-lead stations from García-Martín et al. (DSR submitted) (open symbols). Dotted line represents model II regression lines from the UK–Svalbard stations: $\int CR_{O_2} = 0.1(\pm 0.05)$ $\int GPP + 32.74(\pm 12.05)$, $R^2 < 0.01$, $p=0.89$, $n=6$; and solid line represents the model II regression lines from the ice-lead stations: $\int CR_{O_2} = 0.95(\pm 0.05)$ $\int GPP - 7.57(\pm 5.78)$, $R^2=0.99$, $p<0.001$, $n=4$.

$O_2\ m^{-3}\ d^{-1}$) that reflected the latitudinal changes observed in GPP and chlorophyll, with 83% of samples net autotrophic. The high GPP:CR_{O_2} ratios measured in this study (mean of 4.8 ± 0.7) indicated that most of the organic carbon produced was not respired within the euphotic zone, and was available for transfer to upper levels of the food web or sinking to deeper waters. GPP:CR_{O_2} ratios increased by a factor of 8 from southern to northern stations, yielding the maximum ratios at the most productive stations (CNWS and EGS). The highest values of chlorophyll measured at the northern shelf station (EGS) did not correspond to a higher GPP:CR_{O_2} ratio due to the enhancement of heterotrophic processes. This suggests the presence of bloom or post-bloom conditions at this station characterised by high chlorophyll values with low nitrate+nitrite and high silicate concentrations.

The variability of integrated GPP was four times higher than that of CR_{O_2} across the stations. This relatively homogenous distribution of integrated CR_{O_2} is similar to that previously observed in regional and seasonal studies at mid/low latitudes (Arístegui and Harrison, 2002; del Giorgio and Duarte, 2002; Morán et al., 2004). It has been proposed that differences in the time scale of the autotrophic and heterotrophic processes (Arístegui and Harrison, 2002) may be responsible for this decoupling, particularly the faster response of the photosynthetic processes to episodic nutrient inputs followed by a successive increase in the heterotrophic processes when organic matter is available (Williams et al., 2004). If so, then decoupling would be expected to be greater at small spatial scales which are dominated by intense temporal variability. However, GPP and CR_{O_2} were observed to be closely coupled at short spatial scales in the Arctic during the same research cruise, but subsequent to the current study (García-Martín et al., DSR submitted), as illustrated by the significant 1:1 relationship found in that study (Fig. 8). These scale-dependent differences in the coupling of GPP and CR_{O_2} have important consequences for the prediction of NCP from GPP (Aranguren-Gassis et al., 2011; Serret et al., 2002). Over large geographic scales, the lower variability of CR_{O_2} implies a strong NCP–GPP relationship, allowing NCP to be predicted from GPP. Similar approaches have been used to predict regional to global NCP rates (Duarte et al., 2001; Regaudie-de-Gioux and Duarte, 2010). By contrast, the close coupling and similar variability of both GPP and CR_{O_2} at short spatial scales (as observed in the Arctic by García-Martín et al., DSR submitted) negates the prediction of NCP from GPP alone. GPP:CR_{O_2} relationships therefore appear to be system-dependent (Serret et al., 2002; Serret et al., 2009) and may also be scale-dependent. For example, if the NCP–GPP

relationship found in the present study were to be applied to the Arctic data collected at smaller scales by García-Martín et al. (DSR, submitted), then NCP would have been overestimated as CR_{O_2} rates would not have been considered as a major factor regulating the metabolic balance.

The GPP threshold for metabolic balance (NCP=0) found for this study was 1.5 mmol O_2 m^{-3} d^{-1} which is lower than values previously reported for the North Sea, North Atlantic and Arctic Ocean (3.32, 1.94 and 6.4 mmol O_2 m^{-3} d^{-1}, respectively) by Duarte and Regaudie-De-Gioux (2009). Similarly, the GPP threshold calculated for integrated metabolic balance was 50.52 mmol O_2 m^{-2} d^{-1} which, with a mean euphotic layer of 30 m, is similar to the volumetric threshold. These low thresholds indicate that the planktonic community would be in a net heterotrophic state only at very low values of GPP.

4.2. Heterotrophic processes

The contrasting environmental characteristics of the different stations offered insights into the different factors controlling the bacterial activity. Rates of BP were within the range of previous measurements undertaken in the study area (Reinthaler and Herndl, 2005; Robinson et al., 2002b). The lack of a relationship between BP and temperature along with the close-coupling with GPP, suggests that bacteria were probably controlled by organic carbon release by autotrophs (Thingstad, 2000). Unfortunately, we do not have parallel dissolved organic matter measurements to test if bacterial production was constrained by resource limitation (del Giorgio and Cole, 1998) or by the interaction between temperature and organic carbon (Pomeroy and Wiebe, 2001).

To our knowledge, this is the first study undertaken across contrasting oceanic provinces where CR has been determined simultaneously by *in vitro* changes in dissolved oxygen concentration and by *in vivo* INT reduction assays. The latter method has received criticism from Maldonado et al. (2012) who report that the assay is not specific to enzymes belonging to the electron transport system, and that it could be reduced by other enzymes and abiotic substances present in the cell (thereby not be qualifying as an enzyme assay); they therefore recommended that it should not be used to measure respiration. In the present study, any INT reduction during incubation due to substances derived from abiotic processes could be accounted for by the formalin-killed control but it is possible that some INT reduction may have been due to the activity of enzymes unrelated to the electron transport system. Further, a comparative study of data collected from different oceanographic regions and trophic conditions has revealed a statistically significant relationship between *in vivo* INT reduction and *in vitro* changes in dissolved oxygen consumption (slope of log–log transformed variables = 0.77, $R^2=0.75$, $p<0.0001$, $n>300$). This empirical evidence, combined with the lack of any superior method available to determine BR, suggests that the technique has value as a proxy for estimating respiration, despite its limitations (see García-Martín et al., *in prep*. for further discussion).

A significant regression was observed between CR_{O_2} and CR_{INT}, despite the different incubation times involved (24 h *versus* 2–4 h). This may suggest that the 24 h CR_{O_2} rates were not biased by a non-linear oxygen consumption, which agrees with previous experimental results from mid-latitudes (García-Martín et al., 2011). The large size-fraction community contributed more to the CR_{INT} than bacteria with mean rates 6-fold higher than BR_{INT}; indeed, the contribution of the bacteria never exceeded the contribution of the community of larger size cells. The BR_{INT} rates, converted to units of oxygen using the equation derived from the regression of the two techniques, were low (range 0.16 ± 0.5–2.12 ± 1.1 mmol O_2 m^{-3} d^{-1}) compared to previous rates recorded at these latitudes obtained from oxygen consumption in pre-filtered samples (4.4–30.4 mmol O_2 m^{-3} d^{-1}, Cuevas et al., 2011, and 0.2–8 mmol O_2 m^{-3} d^{-1} assuming a RQ of 1, Reinthaler and Herndl, 2005). Bacterial respiration accounted on average for 24% (range 5–48%) of the total community respiration; lower than the value of 45% proposed by Robinson (2008) but in agreement with values reported from other oceanic systems (25.5 ± 8.5%, Kirchman et al., 2009; 33 ± 7%, Morán et al.,. 2007; 23 ± 4%, Obernosterer et al., 2003). BR values obtained from pre-filtered samples can be expected to be higher than the results from this study as pre-filtration is known to disrupt the plankton community (Gasol and Morán, 1999; Robinson, 2008) and change organic matter availability (Gasol and Morán, 1999) which, in turn, might cause an increase in growth rates of the predator-free bacterial population leading to an overestimation of BR (Aranguren-Gassis et al., 2012). Incubations performed with unaltered plankton communities and short incubation times, as in this study, are expected to provide a more representative picture of the change and variability of BR at high latitudes.

BR_{INT} and its contribution to total CR_{INT} did not differ regionally, and showed no relationship with temperature. These results do not support the conclusion of Rivkin and Legendre (2001) that BR can be estimated from BP and temperature. BGE did exhibit an inverse relationship with temperature ($p<0.05$) but the percentage of variability in BGE attributed to temperature was 36%, lower than the 54% found by Rivkin and Legendre (2001). A positive relationship was observed between chlorophyll and $\%R_{INT}>0.8/CR_{INT}$ which, in combination with the negative relationship between chlorophyll and $\%BR_{INT}/CR_{INT}$, suggests that large eukaryote cells were the major contributors to total CR in chlorophyll-rich waters. In a study conducted in the Atlantic, Arístegui and Harrison (2002) observed that CR was not related to chlorophyll concentration and concluded that bacteria were responsible for the bulk of CR. However, results from this study contradict this conclusion and caution against the assignation of bacteria as the main respiring organisms when total respiration and chlorophyll are not related.

The highest contribution of the large cells to CR_{INT} (> 80%) was found at stations where the GPP was higher than 7 mmol O_2 m^{-3} d^{-1}, and CR_{O_2} ranged between 10% and –30% of the GPP (CNWS and EGS). The percentage of GPP respired by phytoplankton is assumed to be around 35% (Duarte and Cebrian, 1996) which is consistent with phytoplankton blooms, or conditions of high productivity, in which the contribution of heterotrophic organisms, particularly bacteria, to CR is low. This contrasts with other stations (CNS and NNWS) with low GPP and higher CR_{O_2}:GPP ratios, where smaller cells contributed a larger proportion of the CR, typical of microbial-dominated systems. Differences in GPP, CR and the contribution of the bacteria to total CR therefore offer insights into community structure at the different stations.

BR_{INT}, converted to C units using the slope of the regression between CR_{O_2} *versus* CR_{INT} and a RQ of 1 (range 2.3–24.8 mg C m^{-3} d^{-1}), were on average 4-fold higher than BP (range 0.85–4.27 mg C m^{-3} d^{-1}) with no significant relationship observed between both processes. This lack of relationship between BR and BP has been observed in other oceanic regions (Alonso-Sáez et al., 2008; del Giorgio and Cole, 1998; Nguyen and Maranger, 2011) and has been attributed to either methodological problems associated with the longer incubation times required for BR measurement or to different factors controlling the two processes (del Giorgio and Cole, 1998). In the present study BP and BR_{INT} were estimated using similar short incubation times suggesting differential control of BP and BR.

The BGE values observed in this study were derived from the BR_{INT} and BP data and are therefore subject to potential error associated with the estimation of these variables. The limitations of the *in vivo* INT reduction assay used to estimate BR have been discussed above. The use [^{14}C]leucine incorporation to estimate BP is a standard approach but remains subject to uncertainties

associated, in particular, with the conversion of isotope incorporation to BP expressed as carbon units (Ducklow, 2000). The BGE values should therefore be interpreted with caution. BGE was greater than previously reported for temperate waters (del Giorgio and Cole, 1998; Robinson, 2008) but within the range of values recorded from Arctic waters (Nguyen and Maranger, 2011). The BGE values were also highly variable, ranging from 7% to 69%. This variability tended to reflect changes in BR more than BP with highest values observed at the less productive stations where highest BR_{INT} were recorded (SNWS, CNWS and EGS). Interestingly, similar values of BP (*e.g.* as recorded at 5 m depth and at the deep chlorophyll maximum of the CNS and CNWS stations – Table S1) resulted in different values of BGE due to the different BR_{INT}. These results could imply that a constant BGE should not be used to estimate bacterial carbon demand from BP. Instead coupled measurements of BP and BR are required to improve our understanding of the role played by the bacteria in the marine carbon cycle.

In the present study BGE was negatively related to temperature and positively related to chlorophyll and GPP. Some previous studies have reported BGE to be inversely related to temperature (Apple et al., 2006; Kritzberg et al., 2010; Vázquez-Domínguez et al., 2007) while other studies have found no such relationship (Alonso-Sáez et al., 2008; del Giorgio and Cole, 1998; López-Urrutia and Morán, 2007). Interestingly, in those studies where BGE was dependent on temperature, both BP and BR were also related to it. By contrast, BGE increased with decreasing temperature in the present study while neither BP nor BR_{INT} was significantly related to temperature. This suggests that ecological changes related to plankton community structure and functioning, rather than physiological changes, were responsible for variations in BGE with temperature in the present study (del Giorgio et al., 2011). The complex interactions of (a) hydrodynamics with GPP and community structure, and (b) heterotrophic activity, distribution between trophic compartments and efficiency with temperature, productivity and community structure observed in this study suggest that caution should be applied when extrapolating the results of controlled experiments focused on physiological responses to real ecological conditions.

5. Conclusions

This study reveals that GPP was four times more variable than CR along the latitudinal transect between the UK and Svalbard. Depth integrated NCP increased from south to north and was related to increases in GPP and chlorophyll concentration. Plankton metabolism exhibited different patterns of co-variation in both this large-scale study and in a subsequent small-scale study performed in ice-influenced waters (García-Martín et al., DSR submitted), which suggests that NCP may be system and scale dependent; therefore, a universal model should not be used to estimate NCP. BP, BR_{INT} and BGE were highly variable along the transect with no significant relationship observed between BP and BR_{INT}. These results, together with the observation that only BGE, but not BP or BR_{INT}, increased with decreasing temperature support the view that both rate processes could be controlled by different factors, and that ecological rather than physiological changes were responsible for variations in BGE with temperature in the present study.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2014.06.004.

References

Alonso-Sáez, L., Vázquez-Domínguez, E., Cardelús, C., Pinhassi, J., Sala, M., Lekunberri, I., Balagué, V., Vila-Costa, M., Unrein, F., Massana, R., Simó, R., Gasol, J., 2008. Factors controlling the year-round variability in carbon flux through bacteria in a coastal marine system. Ecosystems 11, 397–409.

Apple, J.K., del Giorgio, P.A., Kemp, W.M., 2006. Temperature regulation of bacterial production, respiration, and growth efficiency in a temperate salt-marsh estuary. Aquat. Microb. Ecol. 43, 243–254.

Aranguren-Gassis, M., Serret, P., Fernández, E., Herrera, J.L., Domínguez, J.F., Pérez, V., Escanez, J., 2011. Production and respiration control the marine microbial metabolic balance in the eastern North Atlantic subtropical gyre. Deep-Sea Res. I 58, 768–775.

Aranguren-Gassis, M., Teira, E., Serret, P., Martínez-García, S., Fernández, E., 2012. Potential overestimation of bacterial respiration rates in oligotrophic plankton communities. Mar. Ecol. Prog. Ser. 453, 1–10.

Arístegui, J., Harrison, W.G., 2002. Decoupling of primary production and community respiration in the ocean: implications for regional carbon studies. Aquat. Microb. Ecol. 29, 199–209.

Arrigo, K.R., van Dijken, G., Pabi, S., 2008. Impact of a shrinking Arctic ice cover on marine primary production. Geophys. Res. Lett. 35, L19603, http://dx.doi.org/10.1029/2008GL035028.

Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr. 42 (1), 1–20.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Cuevas, L.A., Egge, J.K., Thingstad, T.F., Topper, B., 2011. Organic carbon and mineral nutrient limitation of oxygen consumption, bacterial growth and efficiency in the Norwegian Sea. Polar Biol. 34, 871–882.

del Giorgio, P.A., Cole, J.J., 1998. Bacterial growth efficiency in natural aquatic systems. Annu. Rev. Ecol. Evol. Syst. 29, 503–541.

del Giorgio, P.A., Cole, J.J., 2000. Bacterial energetics and growth efficiency. In: Kirchman, D.L. (Ed.), Microbial Ecology of the Oceans. Wiley-Liss, New York, pp. 289–325.

del Giorgio, P.A., Condon, R., Bouvier, T., Longnecker, K., Bouvier, C., Sherr, E., Gasol, J.M., 2011. Coherent patterns in bacterial growth, growth efficiency, and leucine metabolism along a northeastern Pacific inshore-offshore transect. Limnol. Oceanogr. 56 (1), 1–16.

del Giorgio, P.A., Duarte, C.M., 2002. Respiration in the open ocean. Nature 420, 379–384.

del Giorgio, P.A., Williams, P.J.l.B., 2005. Respiration in Aquatic Ecosystems. Oxford University, Oxford.

Duarte, C.M., Agustí, S., Aristegui, J., González, N., Anadón, R., 2001. Evidence for a heterotrophic subtropical northeast Atlantic. Limnol. Oceanogr. 46 (2), 425–428.

Duarte, C.M., Cebrian, J., 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41, 1758–1766.

Duarte, C.M., Regaudie-De-Gioux, A., 2009. Thresholds of gross primary production for the metabolic balance of marine planktonic communities. Limnol. Oceanogr. 54, 1015–1022.

Ducklow, H.W., 2000. Bacterial production and biomass in the oceans. In: Kirchman, D.L. (Ed.), Microbial Ecology of the Oceans. Wiley-Liss, New York, pp. 85–120.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281, 237–240.

García-Martín, E.E., Serret, P., Pérez-Lorenzo, M., 2011. Testing potential bias in marine plankton respiration rates by dark bottle incubations in the NW Iberian shelf: incubation time and bottle volume. Cont. Shelf Res. 31, 496–506.

García-Martín, E.E., Serret, P., Leakey R.J.G. Plankton community and bacterial metabolism in Arctic sea ice leads during summer 2010, accepted for publication.

Gasol, J.M., Morán, X.A.G., 1999. Effects of filtration on bacterial activity and picoplankton community structure as assessed by flow cytometry. Aquat. Microb. Ecol. 16, 251–264.
Gosselin, M., Levasseur, M., Wheeler, P.A., Horner, R.A., Booth, B.C., 1997. New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Res. II 44 (8), 1623–1644.
Grasshoff, K., Kremling, K., Ehrhardt, M., 1999. Methods of Seawater Analysis. Wiley-VCH, Weinheim.
Kawasaki, N., Sohrin, R., Ogawa, H., Nagata, T., Benner, R., 2011. Bacterial carbon content and the living and detrital bacterial contributions to suspended particulate organic carbon in the North Pacific Ocean. Aquat. Microb. Ecol. 62, 165–176.
Kiørboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. Adv. Mar. Biol. 29, 1–73.
Kirchman, D., 2001. Measuring bacterial biomass production and growth rates from leucine incorporation in natural aquatic environments. Methods Microbiol. 30, 227–237.
Kirchman, D.L., Hill, V., Cottrell, M.T., Gradinger, R., Malmstrom, R.R., Parker, A., 2009. Standing stocks, production and respiration of phytoplankton and heterotrophic bacteria in the western Arctic ocean. Deep-Sea Res. II 56, 1237–1248.
Kirchman, D.L., Malmstrom, R.R., Cottrell, M.T., 2005. Control of bacterial growth by temperature and organic matter in the Western Arctic. Deep-Sea Res. II 52, 3386–3395.
Kritzberg, E.S., Duarte, C.M., Wassmann, P., 2010. Changes in Arctic marine bacterial carbon metabolism in response to increasing temperature. Polar Biol. 33, 1673–1682.
Legendre, L., Le Fevre, J., 1991. From individual plankton cells to pelagic marine ecosystems and to global biogeochemical cycles. In: Demers, S. (Ed.), Particle Analysis in Oceanography. Springer-Verlag, Berlin, pp. 261–299.
Legendre, L., Rassoulzadegan, F., 1995. Plankton and nutrient dynamics in marine waters. Ophelia 41, 153–172.
Lemée, R., Rochelle-Newall, E., Van Wambeke, F., Pizay, M., Rinaldi, P., Gattuso, J., 2002. Seasonal variation of bacterial production, respiration and growth efficiency in the open NW Mediterranean Sea. Aquat. Microb. Ecol. 29, 227–237.
Longhurst, A., 1998. Ecological Geography of the Sea. Academic Press, Amsterdam.
López-Urrutia, Á., Morán, X.A.G., 2007. Resource limitation of bacterial production distorts the temperature dependence of oceanic carbon cycling. Ecology 88, 817–822.
López-Urrutia, Á., San Martin, E., Harris, R.P., Irigoien, X., 2006. Scaling the metabolic balance of the oceans. Proc. Natl. Acad. Sci. 103, 8739–8744.
Luchetta, A., Lipizer, M., Socal, G., 2000. Temporal evolution of primary production in the central Barents Sea. J. Mar. Syst. 27, 177–193.
Maldonado, F., Packard, T.T., Gómez, M., 2012. Understanding tetrazolium reduction and the importance of substrates in measuring respiratory electron transport activity. J. Exp. Mar. Biol. Ecol. 434–435, 110–118.
Marañón, E., Cermeño, P., Latasa, M., Tadonléké, R.D., 2012. Temperature, resources, and phytoplankton size structure in the ocean. Limnol. Oceanogr. 57, 1266–1278.
Martínez-García, S., Fernández, E., Aranguren-Gassis, M., Teira, E., 2009. *In vivo* electron transport system activity: a method to estimate respiration in natural marine microbial planktonic communities. Limnol. Oceanogr. Methods 7, 459–469.
Michaels, A.F., Silver, M.W., 1988. Primary production, sinking fluxes and the microbial food web. Deep-Sea Res. I 35, 473–490.
Miller, J.C., Miller, J.N., 1988. Statistics for Analytical Chemistry, 5th ed. Pearson Education Limited, Essex, pp. 18–38.
Morán, X.A.G., Fernández, E., Pérez, V., 2004. Size-fractionated primary production, bacterial production and net community production in subtropical and tropical domains of the oligotrophic NE Atlantic in autumn. Mar. Ecol. Prog. Ser. 274, 17–29.
Morán, X.A.G., Pérez, V., Fernández, E., 2007. Mismatch between community respiration and the contribution of heterotrophic bacteria in the NE Atlantic open ocean: what causes high respiration in oligotrophic waters? J. Mar. Res. 65, 545–560.
Nguyen, D., Maranger, R., 2011. Respiration and bacterial carbon dynamics in Arctic sea ice. Polar Biol. 34, 1843–1855.
Obernosterer, I., Kawasaki, N., Benner, R., 2003. P-limitation of respiration in the Sargasso Sea and uncoupling of bacteria from P-regeneration in size-fractionation experiments. Aquat. Microb. Ecol. 32, 229–237.
Pabi, S., van Dijken, G.L., Arrigo, K.R., 2008, C0800. Primary production in the Arctic Ocean, 1998–2006. J. Geophys. Res. 113, C0800, http://dx.doi.org/10.1029/2007JC004578.
Pace, M.L., Cole, J.J., 2000. Effects of whole-lake manipulations of nutrient loading and food web structure on planktonic respiration. Can. J. Fish. Aquat. Sci. 57, 487–496.
Pomeroy, L.R., Wiebe, W.J., 2001. Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria. Aquat. Microb. Ecol. 23, 187–204.
Regaudie-de-Gioux, A., Duarte, C.M., 2010. Plankton metabolism in the Greenland Sea during the polar summer of 2007. Polar Biol. 33, 1651–1660.
Regaudie-de-Gioux, A., Duarte, C.M., 2012. Temperature dependence of planktonic metabolism in the ocean. Glob. Biogeochem. Cyc. 26, GB1015.
Reinthaler, T., Herndl, G.J., 2005. Seasonal dynamics of bacterial growth efficiencies in relation to phytoplankton in the southern North Sea. Aquat. Microb. Ecol. 39, 7–16.
Rey, F., Noji, T.T., Miller, L.A., 2000. Seasonal phytoplankton development and new production in the central Greenland Sea. Sarsia 85, 329–344.
Richardson, K., Markager, S., Buch, E., Lassen, M.F., Kristensen, A.S., 2005. Seasonal distribution of primary production, phytoplankton biomass and size distribution in the Greenland Sea. Deep-Sea Res. I 52, 979–999.
Rivkin, R.B., Legendre, L., 2001. Biogenic carbon cycling in the upper ocean: effects of microbial respiration. Science 291, 2398–2400.
Robinson, C., 2008. Heterotrophic Bacterial Respiration, Microbial Ecology of the Oceans. John Wiley & Sons, Inc., pp. 299–334.
Robinson, C., Poulton, A.J., Holligan, P.M., Baker, A.R., Forster, G., Gist, N., Jickells, T.D., Malin, G., Upstill-Goddard, R., Williams, R.G., 2006. The Atlantic Meridional Transect (AMT) programme: a contextual view 1995–-2005. Deep-Sea Res. II 53, 1485–1515.
Robinson, C., Serret, P., Tilstone, G., Teira, E., Zubkov, M.V., Rees, A.P., Woodward, E.M.S., 2002a. Plankton respiration in the eastern atlantic ocean. Deep-Sea Res. I 49, 787–813.
Robinson, C., Widdicombe, C.E., Zubkov, M.V., Tarran, G.A., Miller, A.E.J., Rees, A.P., 2002b. Plankton community respiration during a coccolithophore bloom. Deep-Sea Res. II 49, 2929–2950.
Robinson, C., Williams, P.J.l.B., 2005. Respiration and its measurements in surface marine waters. In: Del Giorgio, P.A., Williams, P.J.l.B (Eds.), Respiration in Aquatic Ecosystems, (Eds.) Oxford University Press, Oxford, pp. 147–180.
Sakshaug, E., 2004. Primary and secondary production in the Arctic seas. In: Stein, R., Macdonald, R.W. (Eds.), The Organic Carbon Cycle in the Arctic Ocean. Springer, New York, pp. 57–82.
Sampou, P., Kemp, W., 1994. Factors regulating plankton community respiration in Chesapeake Bay. Mar. Ecol. Prog. Ser. 110, 249–258.
Serret, P., Fernández, E., Robinson, C., 2002. Biogeographic differences in the net ecosystem metabolism of the open ocean. Ecology 83, 3225–3234.
Serret, P., Fernández, E., Sostres, J.A., Anadón, R., 1999. Seasonal compensation of microbial production and respiration in a temperate sea. Mar. Ecol. Prog. Ser. 187, 43–57.
Serret, P., Robinson, C., Fernández, E., Teira, E., Tilstone, G., 2001. Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. Limnol. Oceanogr. 46 (7), 1642–1652.
Serret, P., Robinson, C., Fernández, E., Teira, E., Tilstone, G., Pérez, V., 2009. Predicting plankton net community production in the Atlantic Ocean. Deep-Sea Res. II 56, 941–953.
Smith, E.M., Kemp, W.M., 2003. Planktonic and bacterial respiration along an estuarine gradient: responses to carbon and nutrient enrichment. Aquat. Microb. Ecol. 30, 251–261.
Stewart, J.C., Hawcroft, D.M., 1977. A Manual of Radiobiology. Sidgwick and Jackson, London.
Teira, E., Hernando-Morales, V., Martínez-García, S., Figueiras, F.G., Arbones, B., Álvarez-Salgado, X.A., 2013. Response of bacterial community structure and function to experimental rainwater additions in a coastal eutrophic embayment. Estuar. Coast. Shelf Sci. 119, 44–53.
Thingstad, T.F., 2000. Control of bacterial growth in idealized food webs. In: Kirchman, D.L. (Ed.), Microbial Ecology of the Oceans. Wiley-Liss, New York, pp. 229–260.
Tremblay, J.E., Legendre, L., 1994. A model for the size-fractionated biomass and production of marine phytoplankton. Limnol. Oceanogr. 39 (8), 2004–2014.
Vázquez-Domínguez, E., Vaqué, D., Gasol, J.M., 2007. Ocean warming enhances respiration and carbon demand of coastal microbial plankton. Glob. Change Biol. 13, 1327–1334.
Wassmann, P., 1990. Relationship between primary and export production in the boreal coastal zone of the North Atlantic. Limnol. Oceanogr. 35 (2), 464–471.
Williams, P.J.l.B., Morris, P.J., Karl, D.M., 2004. Net community production and metabolic balance at the oligotrophic ocean site, station ALOHA. Deep-Sea Res. I 51, 1563–1578.
Yvon-Durocher, G., Caffrey, J.M., Cescatti, A., Dossena, M., del Giorgio, P., Gasol, J.M., Montoya, J.M., Pumpanen, J., Staehr, P.A., Trimmer, M., 2012. Reconciling the temperature dependence of respiration across timescales and ecosystem types. Nature 487, 472–476.